LAÉRCIO PEIXOTO DO AMARAL NETO

Inferências sobre uma rede de interações abelha-planta: Investigando o papel de polinizadores e pilhadores e a influência da complementaridade fenotípica e de interações proibidas sobre a estrutura e propriedades da rede

Tese apresentada à Coordenação do Programa de Pós-Graduação em Ciências Biológicas, Área de Concentração em Entomologia, do Setor de Ciências Biológicas, da Universidade Federal do Paraná, como requisito parcial à obtenção do título de Doutor em Ciências Biológicas.

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"Inferências sobre uma rede de interações abelha-planta: investigando o papel de polinizadores e pilhadores e a influência da complementaridade fenotípica e de interações proibidas sobre a estrutura e propriedade da rede"

Tese aprovada como requisito parcial para obtenção do grau de "Doutor em Ciências", no Programa de Pós-graduação em Ciências Biológicas, Área de Concentração em Entomologia, da Universidade Federal do Paraná, pela Comissão formada pelos professores:

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RESUMO

A análise de redes mutualísticas é uma ferramenta extremamente útil para a compreensão do nível de interação entre os diferentes subsistemas existentes nos sistemas ecológicos e provê ferramentas que possibilitam a avaliação conjunta de um número grande de variáveis, permitem extrapolar propriedades da rede a sistemas ecológicos e possibilitam extrapolações e predições. Apesar de suas vantagens, alguns trabalhos alertam sobre alguns entraves que podem causar distorções na interpretação dos padrões observados nas redes, entre eles a presença de pilhadores, a variação temporal das interações e a premissa de que todas as interações são igualmente possíveis de acontecer. O presente trabalho explora o efeito destes entraves na estrutura e propriedades de uma rede de interações abelha-planta.

As análises foram feitas a partir dos dados coletados ao longo de dois anos em uma área de campo natural no Parque Estadual de Vila Velha, Ponta Grossa, Paraná. A área foi visitada duas vezes por mês onde foram observadas as interações entre abelhas e plantas atentando-se para os seguintes aspectos: (1) recurso floral utilizado; (2) se o visitante tocava os órgãos reprodutivos da flor; (3) se o mecanismo floral era ativado e; (4) se havia congruência entre o comportamento do visitante e a morfologia da flor. Os visitantes foram então classificados como pilhadores ou polinizadores. Foram registradas também características das flores tais quais: tipo morfológico, cor, simetria, tamanho da flor (profundidade do recurso, altura), recursos disponíveis e coletados e características referentes ao tamanho e comportamento dos visitantes. Esses dados foram usados para confeccionar matrizes baseando-se em diferentes regras explicadas com detalhes em cada capítulo.

O trabalho consta com três capítulos. O primeiro aborda como os polinizadores e pilhadores compartilham os recursos florais. Uma vez que é esperado que os pilhadores diminuam o recurso disponível para os polinizadores e que estes sejam competidores, o objetivo deste capítulo é avaliar se de fato ocorre uma sobreposição de nicho entre as duas funções de visitantes, tanto no sentido das espécies visitadas como nas características das flores. Esta sobreposição de nicho foi avaliada também temporalmente (em cada janela temporal). Nossa hipótese é que quando as visitas de pilhadores e polinizadores são observadas em uma perspectiva de redes, estes dois grupos de visitantes não apresentam uma grande sobreposição de nicho devido à disponibilidade de outros recursos. Os resultados mostraram que polinizadores e pilhadores não apresentam uma grande sobreposição de nicho, sobretudo quanto ao tipo floral e recursos utilizados pelos visitantes. Quando o aspecto temporal é considerado nota-se que apenas uma pequena proporção das espécies de plantas disponíveis é compartilhada. Foi avaliada ainda através de modelos a capacidade de certas combinações de características florais preverem a estrutura da rede baseada na função dos visitantes florais (uma rede onde as espécies de abelhas foram substituídas por sua função, polinizador ou pilhador). Nenhum dos modelos testados foi capaz de predizer a estrutura desta rede função-planta.

O segundo capítulo traz de maneira mais direta uma análise sobre os efeitos em propriedades da rede quando se excluem das análises as visitas de abelhas que não prestam serviços de polinização, ou seja, as espécies pilhadoras. Para isso foram construídas redes de interação com e sem pilhadores para cada janela temporal em que se observou a presença de abelhas que interagiam sem prestar serviços de polinização. Frente aos resultados do primeiro capítulo (que os pilhadores e polinizadores não compartilham muitos dos recursos disponíveis), partiu-se da hipótese de que a retirada dos pilhadores teria pouco efeito nas propriedades da rede. Apenas uma pequena proporção de todas as interações observadas é devida às interações entre plantas e pilhadores (<10%). Entretanto, a retirada dos pilhadores resulta em redes com um menor número de espécies, tanto de plantas como de abelhas, menor valor de

aninhamento e menos especialização média (*d'*) das abelhas. A compartimentalização e índice de especialização das redes (*H2'*) não variaram significativamente, mas foram detectados diferentes efeitos quando cada janela temporal foi analisada separadamente. Esse efeito está relacionado com a posição ocupada pelas interações dos pilhadores na rede.

O terceiro capítulo indaga se a complementaridade fenotípica e as interações proibidas são capazes de predizer as propriedades da rede. Para essa avaliação foram usados modelos onde: (1) as interações entre as plantas e polinizadores eram apenas limitadas pelo encaixe fenológico e morfológico entre as características das flores e das abelhas (nesse caso, um desacoplamento em qualquer das características impede a formação de uma interação e, por isso, essas interações são chamadas "proibidas") ou; (2) pela complementaridade fenotípica (nesse caso eram levadas em consideração as preferências das abelhas por certas características das flores e a falta de complementaridade não impede que a interação ocorra). Uma vez que os grupos funcionais de visitantes florais são definidos baseando-se em várias características, assim como o são as síndromes de polinização complementares a estes grupos funcionais, esperou-se que quanto mais características fossem usadas, mais precisas seriam as predições dos modelos. Baseado nos resultados dos outros capítulos, esperou-se que algumas combinações de características fossem mais efetivas na predição da estrutura das redes, como os recursos coletados, tipo floral e cores. Os resultados mostram que modelos de complementaridade fenotípica são melhores que os modelos que se utilizam de interações proibidas. Também foi observado que combinações de características sempre possuem um melhor desempenho que características isoladas. Modelos que levam em conta apenas a complementaridade fenológica são ruins, embora esta característica aumente o poder de predição dos outros modelos quando usada conjuntamente.

De maneira geral essa tese apresenta alguns efeitos e traz discussões sobre dois aspectos que podem interferir na interpretação dos resultados em estudos de redes: A presença de pilhadores e as interações proibidas. Apesar dos estudos de redes possuírem a vantagem de permitir generalizações sobre um sistema e a análise de grandes conjuntos de dados, o estudo mais detalhado das interações envolvidas pode trazer respostas em que apenas os padrões e métricas da rede não seriam suficientes. No que se refere aos pilhadores, este foi o primeiro trabalho com redes em um aspecto mais amplo para testar seu efeito. Trabalhos prévios focam observações centradas em uma espécie de planta ou uma família de plantas. Foi demonstrado que, embora estas representem apenas uma pequena proporção de interações e que compartilhem poucas espécies com os polinizadores, a exclusão de interações entre pilhadores e flores altera algumas propriedades da rede. Mesmo as métricas que parecem não ser afetadas pela exclusão dos pilhadores sofrem interferências variáveis quando analisadas em menores escalas temporais, mostrando a importância da distinção deste tipo de comportamento nos estudos de redes.

O efeito das interações proibidas é um tema recorrente em trabalhos de redes atuais onde se avalia a complementaridade fenológica e morfológica das espécies que interagem como determinantes dos padrões observados. No entanto o presente estudo tem como principal novidade o uso de uma quantidade comparativamente maior de características morfológicas de ambos os lados, abelhas e plantas, além de incluir a complementaridade fenotípica. Concluiu-se que as características morfológicas podem ter uma importância maior quando mais características são incluídas, o que possivelmente deve-se ao fato de proporcionar uma maior descrição do encaixe funcional entre as espécies.

Palavras-Chave: Melitofilia; acoplamento fenológico; interações mutualísticas; métricas de rede; pilhadore; polinizadores; interações proibidas.

ABSTRACT

The analysis of mutualistic networks is an extremely useful tool for understanding the level of interaction between existing subsystems of ecological systems and provides tools that enable evaluation of a large number of variables, extrapolation the network properties to ecological systems and predictions about evolution of the ecological systems. Despite its advantages, some studies warn of some barriers that may distort the interpretation of patterns observed in the networks, including the presence of robbers, the temporal variation of the interactions and the assumption that all interactions are possible to happen. This paper explores the effect of these barriers in the structure and properties of a network of bee-plant interactions.

Analyses were made from data collected over two years in a natural field area in the Vila Velha State Park, Ponta Grossa, Paraná. The area was visited twice a month where they were observing the interactions between bees and plants paying attention to the following aspects: (1) used floral resources; (2) if the visitor played the reproductive organs of the flower; (3) if the mechanism was activated and floral; (4) whether there was coherence between visitor behavior and morphology of the flower. The visitors were then classified as robbers or pollinators. It was also recorded characteristics of such flowers which: morphological type, color, symmetry, flower size (depth of resource, height), available resources and collected and characteristics relating to the size and behavior of visitors. These data were used to produce matrices based on different rules explained in detail in each chapter.

This work comprises three chapters. The first addresses how pollinators and robbers share the floral resources. Since it is expected that the robbers reduce the resource available to pollinators and they are considered competitors, the purpose of this chapter is to assess whether in fact there is a niche overlap between the two functions of visitors, both in the sense of species visited as in characteristics of flowers. This niche overlap was also evaluated temporally (for each temporal window). Our hypothesis is that when the robbers' and pollinators' visits are observed in a network perspective, these two groups of visitors do not have a large niche overlap because of the availability of other resources. The results showed that, especially as the floral type and resources used by visitors, pollinators and robbers do not have a large niche overlap. When the temporal aspect is considered noted that only a small proportion of species of plants available is shared. It was also assessed through models the ability of certain combinations of floral traits predict the structure of the network based on the function of floral visitors (a network where the bee species were replaced by their function, pollinator or nectar thief). None of the models tested was able to predict the structure of this function-plant network.

The second chapter brings more directly an analysis of the effects on the network properties when it excludes from the analysis the visits of robbers. For this, interaction networks were built with and without robbers for each time window in which it was observed the presence of bees interacting without paying pollination services. Based on the results of the first chapter (the robbers and pollinators do not share many of the available resources), it started with the assumption that the withdrawal of the robbers would have little effect on the network properties. Only a small proportion of all the interactions observed are due to interactions between plants and robbers (<10%). However, the removal of the robbers results in networks with a smaller number of species, both plant as bees, lower nesting less-skilled and (*d* ') of bees. The compartmentalization and networks specialization index (*H2* ') have not varied significantly, but were detected different effects when each time window was analyzed separately. This effect is related to the position occupied by the interactions of the robbers on the network.

The third chapter asks whether the trait complementarity and forbidden links are able to predict the properties of the network. For this evaluation were used models where: (1) the interactions between plants and pollinators were only limited by phenological and morphological

fit between the characteristics of flowers and bees (in this case a decoupling in any of the characteristics prevents the formation of an interaction and therefore, these interactions are called " forbidden links "), or; (2) the trait complementarity (in this case are taken into account the preference for certain characteristics of the bees from flowers and the lack of complementarity does not prevent the interaction occurs). Since the functional groups of flower visitors are defined based on various characteristics, as are the complementary pollination syndromes to these functional groups, it was expected that the more characteristics were used, they would be the most accurate predictions of the model. Based on the results of the other chapters, it was expected that some characteristics combinations were more effective in predicting the structure of the networks, as the collected resources, floral type and colors. The results show that trait complementarity models that are better than forbidden links models. It was also noted that combinations of characteristics always have a better performance than isolated features. Models that take into account only the phenological complementarity are the worst, although this feature increases increases the predictive power of other models.

Overall this thesis presents some effects and shed some light on two aspects that can interfere with the interpretation of the results in network studies: The presence of robbers and prohibited interactions. Although networks has the advantage of allowing a system and generalizations about the analysis of large data sets studies, more detailed study of the interactions involved can provide responses that only patterns and network metrics would not be enough to respond. With regard to robbers, this was the first work with networks in a broader aspect to test its effect. Previous studies focused observations centered on a species of plant or plant family. It has been shown that although these represent only a small proportion of interactions and share few species with pollinators, excluding interactions between robbers and flowers amending certain network properties. Even metrics that do not seem to be affected by the exclusion of robbers suffer variable interference when analyzed in smaller time scales, showing the importance of distinguishing this type of behavior in studies of networks.

The effect of forbidden links is a recurring theme in interaction networks where it is evaluated the phenological and morphological complementarity of species that interact as determinants of the observed patterns. However, the present study has as main novelty the use of a comparatively larger amount of the morphological characteristics of both sides, bees and plants, and includes trait complementarity. It was concluded that the morphological characteristics may have an increased importance as more features are included, which is probably due to the fact that a further description of the functional fit between species.

Keywords: melittophily; phenological coupling; mutualistic interactions; network metrics; robbers; pollinators; forbidden links.

INTRODUÇÃO GERAL

Especialização e generalização entre polinizadores e plantas

Evidências paleontológicas indicam que a co-radiação dos grupos de insetos visitantes florais e as angiospermas iniciou-se no Cretáceo (Grimaldi 1999), precedidos no fim do Jurássico e inicio do Cretáceo por insetos com partes bucais mastigadoras ou picadoras, provavelmente utilizadas para alimentação de seiva ou pólen de gimnospermas (Labandeira 1997; 1998). A interação com as flores levou a uma série de adaptações nos insetos visitantes, tanto morfológicas como comportamentais (Jander 1976; Niv et al. 2002; Krenn et al. 2005; Cakmak et al. 2009). Em relação às plantas, estas também apresentam combinações das características florais ou "síndromes de polinização" que podem ser usadas para se inferir seus polinizadores (Darwin 1877; Faegri and Pijl 1979; Johnson & Steiner 2000) e seriam resultado de uma evolução conjunta entre insetos e plantas (Fenster et al. 2004).

De acordo com o conceito de síndromes de polinização, as flores de várias angiospermas apresentam uma série de características que refletem as adaptações a um grupo específico de animais visitantes (Waser et al. 1996; Fenster et al. 2004). A ideia de síndrome, no entanto, tem sido questionada com base em evidências de uma ampla generalização dos sistemas de polinização, pois espécies vegetais são visitadas por um amplo espectro de animais cujas características muitas vezes não correspondem com as síndromes apresentadas pelas flores (Ollerton 1996; Waser et al. 1996; Johnson & Steiner 2000; Obermuller et al. 2008; Ollerton et al. 2009). Essas críticas ganham força com o advento do estudo de comunidades de polinizadores e plantas por meio das redes de interações, as quais mostram a tendência de que mesmo espécies de plantas com flores que apresentam restrições morfológicas aos visitantes interagirem com uma grande gama de animais (Jordano et al. 2003; Bascompte & Jordano 2007).

Frente a estes fatos, alguns autores defendem os conceitos de “síndromes” e “especialização nos sistemas de polinização” ampliando sua interpretação. Dessa forma a especialização nos sistemas de polinização se refere ao fato de plantas serem polinizadas por um grupo menor de espécies de visitantes, com características e comportamentos

semelhantes, os quais podem ser agrupados em grupos funcionais (Armbruster et al. 2000; Fenster et al. 2004). Assim, mesmo que as plantas sejam visitadas por vários animais, e aparentemente sejam generalistas, a guilda de visitantes possui em comum um conjunto mais restrito de características que direciona a evolução floral.

Além disso, as interações entre plantas e seus polinizadores ocorrem imersas em uma teia de interações que envolvem várias espécies que compõem uma comunidade. Dessa forma a evolução dessas interações ocorre de maneira mais dinâmica, em que vários fatores que não apenas as interações par-a-par estão envolvidos. Por exemplo, se uma espécie de planta possui muitos visitantes diferentes que proveem serviços similares de polinização, e se os custos dessas interações são comparáveis, há pouco incentivo para que uma planta se especialize em atrair apenas um grupo particular de polinizadores (Mitchell et al. 2009). Por outro lado, se alguns dos visitantes florais são mais efetivos na quantidade ou qualidade do pólen transferido, a seleção favoreceria caracteres que promovessem esses polinizadores mais efetivos (Jonhson et al., 1998, Medel et al., 2007, Muchhala et al., 2009). Os visitantes, sobretudo os insetos, tendem a ser mais generalistas, pois visitam as flores por recursos variados, sendo necessário visitar espécies diferentes para cada tipo de recurso. Ainda assim, quando apenas um recurso é levado em consideração, os insetos parecem exibir uma tendência a maior especialização (Bezerra et al., 2009, Pauw, 2006). Logo, para se entender os padrões de generalização e especialização, é necessária uma compreensão de vários aspectos das comunidades (Waser et al. 1996; Johnson & Steiner 2000) e não apenas as relações par-a-par, como nos estudos mais clássicos em interações ecológicas.

Compreender os aspectos de toda a comunidade de polinizadores e suas plantas, no entanto, não é uma tarefa fácil. Apesar disso, uma ferramenta tem ganhado destaque nos últimos anos que contribui de sobremaneira com os estudos das comunidades de planta-polinizadores: a abordagem de redes complexas.

Estudos de redes de interação

Redes de interação consistem em conjuntos de nós (por exemplo, espécies) conectadas através de conexões (*links*), cada um correspondente a uma associação entre dois

nós (Bascompte & Jordano 2007). Mais especificamente, as redes de polinização representam as interações entre as plantas e os animais visitantes em uma determinada localidade. Os estudos de redes em geral derivam-se da descrição topológica de redes complexas a partir da teoria dos grafos de Erdös e Rényi e inicialmente foram usados para descrever redes de informação, redes sociais e, posteriormente utilizados em sistemas biológicos (Barabási & Albert 1999; Albert & Barabási 2002).

A abordagem de redes em ecologia tem uma tradição maior nos estudos de ecologia de comunidades e redes alimentares, onde tem sido utilizada por mais de 40 anos (Paine 1966; Pimm et al. 1991; Menge 1995). Mais tarde, no entanto, surge uma tendência de se utilizar dessa abordagem em estudos de interações mutualísticas entre plantas e polinizadores, dispersores de sementes e plantas e formigas inquilinas (Bascompte et al. 2003; Guimarães et al. 2007). Atualmente a análise de redes ecológicas tem sido largamente utilizada, reavivando as observações "descritivas" das interações no contexto das comunidades naturais (Blüthgen 2010). Esse tipo de abordagem pode prover informações importantes no estudo de comunidades que não podem ser obtidas quando as espécies são estudadas de maneira isolada. Tal importância reside no fato de que não podemos compreender o funcionamento de sistemas megadiversos focando os estudos em espécies isoladas, já que o comportamento de todo o sistema mostra propriedades que vão além da soma de suas partes (Jordano et al. 2009; Blüthgen 2010). Os estudos de redes mutualísticas ou teias alimentares, diferentemente dos estudos tradicionais em ecologia das interações, procuram uma compreensão maior do ecossistema como um todo (Bascompte & Jordano 2007) e não apenas das relações entre um grupo pequeno de espécies. A análise de redes é uma ferramenta extremamente útil para a compreensão do nível de interação entre os diferentes subsistemas existentes nos sistemas ecológicos (Benedek et al. 2007) e provê ferramentas que possibilitam a avaliação conjunta de um número grande de variáveis, permitindo extrapolar propriedades da rede a sistemas ecológicos e dando aos estudos possibilidade de extrapolações e predições.

Uma das contribuições mais importantes para os estudos de redes biológicas complexas foi o reconhecimento de que, independentemente da natureza dos nós, as redes em geral mostram propriedades estatísticas semelhantes. Dessa forma, sua topologia e evolução

podem estar relacionadas a regras que regem sua organização (Albert & Barabási 2002; Jordano et al. 2003). A abordagem de redes então se baseia na análise de uma ou poucas dessas propriedades estatísticas ou métricas (Bascompte & Jordano 2007 e Blüthgen et al., 2008) para compreender o sistema como um todo e quais as consequências dos padrões observados para a estrutura da comunidade e evolução das espécies.

O que as métricas podem revelar

Uma das propriedades das redes mutualísticas é que estas tendem a mostrar um significativo padrão aninhado onde as espécies especialistas interagem com um subgrupo das espécies que interagem com generalistas (Bascompte et al. 2003). Esse padrão pode ser explicado por uma tendência de que, quando um novo nó é adicionado a uma rede existente, este se liga preferencialmente a uma espécie generalista (Barabási & Albert 1999). Essa ideia de "ligação preferencial" (*preferencial attachment*) das novas espécies na rede interagirem com espécies bem conectadas foi testada em modelos de redes auto-organizáveis (*self-organizing network model* - SNM) que revelaram que esta tendência de fato resulta em um padrão aninhado (Medan et al. 2007).

Foi demonstrado que um padrão aninhado diminui a competição e aumenta o número de espécies coexistentes (Bascompte et al. 2006; Bastolla et al. 2009), e redes que apresentam esse padrão são mais resistente às extinções (Memmott et al. 2004; Burgos et al. 2007; Thébault & Fontaine 2009) e à perda de habitat (Fortuna & Bascompte 2006). A maior resiliência em comunidades com o padrão aninhado se deve ao fato de que, frente à perda de espécies especialistas (*ex*. um polinizador), o parceiro mutualístico remanescente (*ex*. uma espécie de planta) pode contar com outras espécies mais generalistas. No entanto essa resiliência pode estar associada com a sequência em que as extinções ocorrem em uma rede aninhada, sendo que a eliminação preferencial de espécies mais especialistas resulta em uma menor desestruturação da rede (Burgos et al. 2007). Por outro lado, uma tendência à eliminação das espécies mais conectadas da rede faz com que estas entrem rapidamente em colapso (Burgos et al. 2007).

O padrão aninhado e assimétrico das redes mutualísticas pode ser explicado pela hipótese da complementaridade de traço ou das ligações proibidas (Santamaría & Rodriguez-Gironés 2007; Rezende et al. 2007). De acordo com essas ideias, nem todas as interações em uma comunidade podem acontecer devido à existência de restrições fenológicas e morfológicas entre as espécies. De fato alguns trabalhos têm revelado que o padrão observado em redes mutualísticas pode ser influenciado por uma série de fatores, como restrições morfológicas, abundância, fenologia e proximidade filogenéticas entre as espécies que interagem (Rezende et al. 2007; Krishna et al. 2008; Vázquez et al. 2009b; Maruyama et al. 2014).

Além do padrão aninhado, muitas das redes mutualísticas apresentam uma estrutura compartimentalizada onde um grupo de espécies (compartimentos ou módulos) possui mais ligações entre si do que com espécies de outros grupos (Olesen et al. 2007; Vázquez et al. 2009a). Alguns trabalhos têm inclusive demonstrado que as redes apresentam ao mesmo tempo um padrão aninhado e compartimentalizado (Olesen et al. 2007; Fortuna et al. 2010). Assim como o aninhamento, os módulos supostamente também aumentam a estabilidade de redes tróficas, mas possuem apenas um pequeno efeito na estabilidade de redes mutualísticas (Olesen et al. 2007; Thébault & Fontaine 2009; Stouffer & Bascompte 2011). Nesse caso a estabilidade se deve ao poder dos módulos de restringirem os efeitos de distúrbios aos compartimentos, evitando ou retardando os efeitos para o restante da rede. Os módulos podem ainda corresponder a unidades onde uma seleção recíproca de características ocorre mais fortemente, e os compartimentos corresponderiam assim às síndromes de polinização (Olesen et al. 2007; Danieli-Silva et al. 2012).

A especialização sempre foi um tema central nas interações mutualísticas e com o advento dos estudos de rede não é diferente. Entender o quanto as interações dentro de uma comunidade são especializadas e o grau de especialização das espécies que compõem essa comunidade continuam uma das preocupações nos estudos de redes. Uma das métricas usadas para medir a especialização da rede é a conectância, que corresponde à proporção do número de conexões (*links*) observados pelo total de conexões (*links*) possíveis da rede. Dessa forma, quanto mais próximo de que cada um dos animais de uma comunidade estiver de

interagir com todas as plantas disponíveis, mais conectada e, consequentemente, mais generalista é a rede. Como uma medida de especialização e do quanto as espécies estão conectadas, redes mais conectadas teoricamente seriam também mais bem estruturadas contra a extinção de espécies e redes mais especializadas (menos conectadas) sendo mais sujeitas à extinção de seus componentes (Dunne et al. 2002). No entanto um levantamento da relação entre conectância e o valor da comunidade para a conservação (onde comunidades pós-distúrbio possuem menores valores para conservação), em comunidades sujeitas a diferentes tipos de degradação, mostrou que o efeito desta é variável (Heleno et al. 2012). Por conseguinte, a conectância não representa uma boa medida da importância para conservação das comunidades. Entre os problemas associados a esta métrica estão o fato de que ela leva em consideração apenas a presença ou ausência das interações (qualitativa) e é bastante sensível ao tamanho da rede e esforço amostral (Blüthgen et al. 2007). Além disso, a conectância é um índice que se baseia na ideia de que todas as interações são possíveis (uma vez que a conectância máxima é obtida se todas as espécies de um grupo, *ex.* abelhas, interagem com todas as espécies do outro grupo, *ex.* plantas), resultando de encontros ao acaso entre indivíduos (neutralidade das interações).

Em contraste, o índice de especialização H'_2 (baseado na entropia de Shannon) leva em consideração a frequência com que as interações são observadas (quantitativo). Esse índice mede a complementaridade (ou exclusividade) dos nichos ocupados pelas espécies observadas e o quanto a distribuição das interações desvia da neutralidade. Se em uma rede de polinização os visitantes possuem pouca sobreposição de nicho, isto é, visitam plantas diferentes, o índice de especialização da rede H'_2 consequentemente aumenta. Esse índice apresenta várias vantagens, entre elas ser menos sensível ao tamanho da rede e ao esforço amostral e levar em conta o número de observações de cada interação.

Alguns índices ao nível das espécies também merecem destaque e estão associados aos padrões observados ao nível de rede. O mais simples de todos é o grau da espécie, que indica o número de associações de uma determinada espécie. Geralmente observamos na rede um padrão de distribuição de grau onde várias espécies possuem muitas conexões e poucas possuem um número reduzido de interações, resultando algumas vezes no padrão

aninhado (Albert & Barabási 2002; Bascompte et al. 2003). Apesar de simples, essa medida é um bom ponto de início para compreensão das interações das espécies e para comparações com índices mais complexos (Benedek et al. 2007). O índice de especialização da espécie *d'* está relacionado com o H'_2 e também é um índice quantitativo. Uma vantagem do *d'* é que ele considera não só a diversidade de parceiros mutualísticos, mas também suas respectivas disponibilidades (Blüthgen et al. 2006; Blüthgen 2010). De maneira simplificada a especialização de uma espécie depende então de dois fatores: (1) a espécie interage com poucos parceiros (especialista) e, (2) estes parceiros não são os mais abundantes na comunidade. Por último, a força de uma espécie é uma medida de quanto ela depende de seus parceiros mutualísticos. A força de um visitante floral, por exemplo, é calculada como a soma das dependências deste por cada uma das plantas que ele visita para obter os recursos (Bascompte et al. 2006). Ainda como um resultado do padrão aninhado, Bascompte e colaboradores (2006) observaram que as redes mutualísticas apresentam um padrão assimétrico de dependências onde as espécies com altos valores de dependência por seus parceiros tendem a interagir com espécies que pouco dependem delas.

Apesar da importância destas e de outras métricas e da relação da topologia da rede com as propriedades da comunidade que podem ser inferidas a partir delas, o estudo de redes complexas possui algumas falhas. Certos aspectos da biologia e ecologia das interações não são levados em consideração durante a interpretação dos resultados da topologia das redes. Dessa forma, a simplificação dos sistemas naturais por meio de modelos, que representa uma das maiores vantagens na utilização dessa abordagem, passa a representar também uma série de entraves que podem comprometer a sua interpretação ecológica.

Alguns entraves na interpretação ecológica das métricas

Alguns trabalhos alertam sobre os entraves que podem causar distorções na interpretação dos padrões observados nas redes. Entre estes entraves estão: o efeito causado por espécies raras, que sempre aparecem como dependentes ou especialistas; efeitos de amostragem como curtos períodos ou perspectiva focada nas plantas, e métricas susceptíveis a estes; supressão da dinâmica espaço-temporal das interações na comunidade entre outros

(Bosch et al. 2009; Vázquez et al. 2009a; Blüthgen 2010; Blüthgen & Klein 2011). Aqui focaremos em três outros aspectos.

As interações representadas nas redes de interação nem sempre correspondem à função considerada, por exemplo, as interações entre plantas e visitantes florais em redes de polinização que não correspondem a um evento de polinização (Blüthgen & Klein 2011). Nas redes de polinização, o termo "polinizador" é usado como um termo genérico para todos os tipos de visitantes florais (Elberling & Olesen 1999; Basilio et al. 2006; Olesen et al. 2008). Dessa forma, muitas das conexões formadas nessas redes não se constituem verdadeiras interações entre plantas e seus polinizadores (Genini et al. 2010).

Outros autores ressaltam os possíveis efeitos dos pilhadores nas redes (Irwin et al. 2001; Genini et al. 2010). Irwin e colaboradores (2001) propõem alguns desses efeitos como, por exemplo, os pilhadores podem contribuir para a persistência em longo prazo das comunidades exercendo um papel estabilizador nesses sistemas de interação. Em uma matriz com várias plantas, os polinizadores possivelmente evitariam as plantas mais pilhadas e com menos recursos e, dessa forma, aumentariam a taxa de visitação em outras plantas (Irwin et al. 2001). Essa diferença no nicho realizado dos visitantes florais seria refletida na topologia da rede. Entretanto os autores alertam que os efeitos dos pilhadores em uma comunidade não foram explorados. Uma abordagem de redes por Genini e colaboradores (2010) comparou redes de visitantes florais e encontraram que as redes que incluíam pilhadores exibiam uma maior modularidade e que estes estavam mais dispersos dentro dos módulos do que entre eles. Entretanto os autores focaram seu estudo em duas famílias de plantas, e não em toda a comunidade de plantas e visitantes florais.

A variação temporal geralmente não é avaliada nas redes de interação. Petanidou e colaboradores (2008) acompanharam por quatro anos consecutivos uma comunidade de plantas e visitantes florais. Eles observaram que tanto a composição de espécies como as interações formadas entre as espécies variaram ao longo dos anos. Isso teria várias consequências para as métricas de rede, pois espécies que aparecem como especialistas em um ano tendem a ser generalistas ou fazerem interações com outros parceiros mutualísticos no ano seguinte. Dessa forma as redes são muito mais resilientes do que aparentam, dada a

natureza oportunística de plantas e animais em utilizarem os recursos disponíveis. Um padrão semelhante foi observado em outro estudo onde os autores notaram que, apesar da variação nos pares de espécies que interagem, a estrutura aninhada permaneceu constante nos três anos de estudo (Alarcón et al. 2008). Os autores concluem que este aspecto dinâmico da comunidade, em detrimento à topologia constante da rede observada, possui várias implicações tanto ecológicas como evolutivas nas interações de polinização. Assim uma melhor compreensão da dinâmica da comunidade é alcançada quando a rede é estudada em janelas temporais.

A última distorção é a premissa de que todas as interações em uma rede são igualmente possíveis de acontecer. Duas hipóteses podem ser invocadas para contradizer essa ideia: a hipótese da "abundância–assimetria" (Vázquez & Aizen 2004; Vázquez et al. 2007) e a hipótese da "complementaridade fenotípica" (Jordano et al. 2003; Santamaría and Rodriguez-Gironés 2007). A hipótese da abundância–assimetria baseia-se nos seguintes pressupostos: (1) Todas as interações em uma rede são possíveis de ocorrer, (2) as interações ocorrem entre um par de espécies ao acaso, logo (3) se os indivíduos de uma comunidade interagem ao acaso, a abundância das espécies determina a frequência e a força das interações interespecíficas, resultando na estrutura assimétrica das redes (Vázquez et al. 2007). Tal hipótese foi testada pelos próprios autores que concluíram que apenas a abundância das espécies não pode ser usada como regra geral para o padrão aninhado das redes complexas, embora possa fornecer explicação suficiente para algumas redes (Vázquez et al. 2007). A hipótese da "complementaridade fenotípica" ou das "interações proibidas" (Jordano et al. 2003) estipula que a formação das conexões está associada com os atributos biológicos das espécies. Por exemplo, não é possível de uma interação ocorrer entre uma planta e um animal cuja fenologia ou traços fenotípicos sejam díspares. Quanto mais características fenotípicas das espécies são consideradas, maior é a semelhança topológica de uma rede gerada artificialmente com as redes naturais (Santamaría and Rodriguez-Gironés 2007; Rezende et al. 2007).

Na verdade as duas hipóteses não são excludentes e uma série de trabalhos mais recentes busca entender quais destas e ainda quais outras causas resultam nos padrões

observados na rede. Estes trabalhos buscam por meio de metodologias diferentes revelar o quanto a abundância, a complementaridade fenológica, morfológica e espacial das espécies podem predizer as métricas observadas (Vázquez et al. 2009b; Junker et al. 2013; Eklöf et al. 2013; Maruyama et al. 2014; Vizentin-Bugoni et al. 2014; Olito & Fox 2014). Estes trabalhos se utilizam de modelos que representam uma simplificação do sistema para aquelas únicas variáveis que se intenciona testar. Esses trabalhos têm revelado graus de importância variáveis para cada característica avaliada, embora seja uma tendência que modelos que envolvem combinações entre abundância e algum tipo de complementaridade, seja morfológica ou espaço-temporal, são geralmente os melhores e, em alguns casos apenas uma ou poucas característica sejam o suficiente pra prever a estrutura das redes (Vázquez et al. 2009b; Eklöf et al. 2013; Olito & Fox 2014).

Um retorno aos estudos de interação par-a-par?

No início desta introdução discutimos que as interações não ocorrem isoladas e por isso deveriam ser estudadas em um espectro mais amplo. Em contrapartida a seção anterior demonstra alguns dos riscos da utilização das ferramentas de redes sem uma compreensão da natureza das interações e das espécies envolvidas. O fato de que o comportamento de todo o sistema mostra propriedades que vão além da soma de suas partes não exume o fato de que as partes é que formam o todo. Dessa forma, mesmo com as ferramentas proporcionadas pela abordagem de redes para o estudo de processos evolutivos e ecológicos ao nível de comunidade, uma tradução clara dos padrões observados é necessária de modo a não comprometer a compreensão dos sistemas.

Tendo em vista as discussões apresentadas, o presente trabalho tem o objetivo de avaliar o efeito de alguns desses entraves na estrutura topológica de uma rede de abelhas e plantas visitadas por estas, sobretudo: o efeito dos pilhadores na rede e como estes compartilham o recurso com os polinizadores; qual a dinâmica dessas interações frente à variação temporal; e quais os efeitos da complementaridade de traço e das ligações proibidas nas interações entre abelhas e plantas.

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CAPÍTULO I

Como os polinizadores e pilhadores compartilham os recursos florais em uma rede de interações abelha-planta*

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How do pollinator and robbers share floral resources in a bee-plant network?

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Abstract

Bees are not only among the most important pollinators but also correspond to the most important floral larcenists, obtaining floral resources without providing pollination services. Since robbers reduce the available resources for pollinators, these floral visitors are considered competitors. However, the extent of the effects of those interactions in a community context, where many other plants may provide resources, and considering that bees may exhibit a large niche breadth, remains unexplored. We studied bee-plant interactions from a grassland vegetation community observed for two years and used a network approach to investigate the pattern of niche partitioning between pollinators and robbers concerning flower traits and resources collected. We also evaluated the temporal variation in niche overlap by comparing linkage properties of pollinators and robbers for each temporal window sampled. Finally we investigated whether flower traits and phenological constraints are able to predict metrics from function-plant network. Pollinators and robbers had strong niche partitioning regarding flower morphology and resource collected. They also exhibit some degree of specialization for others flower traits, excepted for symmetry. We found that pollinators and robbers share only a small proportion of available plant species (less than 15%) and for a great proportion of the temporal windows they showed no overlap. Flower types alone and models incorporating them were the best predictors of network properties, with color model as the best predictor of observed pairwise interactions. Our results suggest that pollinators are not strong competitors, especially when time variance in interactions are observed, and that flower morphology exerts strong influence on the niche partitioning between those kinds of flower visitors.

Introduction

Bees and plants have long been described as mutualistic partners, with bees serving as a vector for plant male gametophytes while foraging for food and other flower resources. Nevertheless, interactions between bees and flowers are not always a “bed of roses”. Bees are also among the most important group of floral larcenists, in others words, animals that collect flower resources without providing pollination services (Inouye, 1980; Irwin et al., 2010). Floral larcenists are usually described as ‘cheaters’ of plant-animal mutualisms in several studies due to their ability to obtain resources without pollinating (Maloof e Inouye, 2000; Irwin et al., 2001; Genini et al., 2010). However the effect of these visitors on plants are variable, ranging from negative to neutral or even positive (Maloof and Inouye 2000), although it seems that an overall detrimental effect is more common (Irwin et al., 2010).

The studies on effects of cheaters usually focus on its effects on plant reproduction (Stout et al., 2000; Maloof, 2001; Dedej e Delaplane, 2004; Irwin et al., 2010; Mayer et al., 2014) and the effect of flower larceny on the behavior of the flower-visitor guild (Irwin e Brody, 1998; Richardson, 2004; Zhang et al., 2014). These studies usually point robbers as competitors of other flower visitors, pollinators and other larcenists, by depleting available floral resources from visited flowers (Roubik, 1982; Irwin et al., 2010; Wang et al., 2013).

Despite the growing knowledge about the effects of robbery on plant species and its visitors, the community-level aspects of those interactions remains so far unexplored. Usually the studies on floral larceny focus on populations of a single plant species. Nevertheless, interactions between plants, pollinators and larcenists are embedded in a larger web of interactions, and the presence of cheaters may influence community-level dynamics (Irwin et al., 2001; Bascompte e Jordano, 2007).

In flower-visitor networks, interactions are interpreted as components of ecological niches in such a way the niche breath of animals are defined as the spectrum of plants visited, and the degree of niche partitioning corresponds to the extent on how they share their interaction partners (Blüthgen et al., 2006; Junker et al., 2013). Changing the perspective of studies from the traditional observations focused on single plant species to a broader view of interacting networks may help to detect the processes determining the visitation niches of pollinators and flower larcenists. Another neglected aspect on robbery studies is the temporal

variation of those interactions. Once studies are focused on plant species, the interactions between plants and flower visitors are studied in the temporal window restricted by a given plant flowering time. However temporal dynamics of species in the communities, including abundance variation and changes in observed pairwise interactions, contribute to observed patterns in networks (Olesen et al., 2008; Vázquez et al., 2009; Olito e Fox, 2014), and the same should be true to the patterns of interactions between pollinators and robbers.

In the present study we used a network approach in order to understand: (1) how is the pattern of niche partitioning between pollinators and robbers concerning the plant species and flower traits? Are they strong competitors (great niche overlap) as suggested by studies focused on plant species or exhibit any degree of niche complementarity? (2) How do temporal aspects affect the niche partitioning between pollinators and robbers? (3) If flowers traits are important to define bee's function, could they predict the kind of visit, either robbery or pollination, and niche partitioning properties? We expect that in a broad community context, as used in the present study, the competition effects between pollinators and robbers for resources and specific flower traits would be reduced once there would be many other plant species that can be explored by pollinators. Thus, robbers and pollinators would be more prone to niche partitioning instead of a strong competition due to niche overlap. If this statement is correct and there are flower traits more related to each function of flower visitors, we also expect that models based on those traits are able to predict the properties of our function-plant network.

Material and Methods

Study system and sampling methods

We studied flower visitation by bees in natural grasslands at the State Park of Vila Velha, Ponta Grossa, Paraná, Brazil for two years, from August 2011 to August 2013. The study site is located around the coordinates 25°14'13"S and 49°59'58"W, at 900-910 m above sea level (for further details see Gonçalves et al. 2009) and was subdivided into four contiguous plots of 50 x 50m each for sampling purposes. We visited the study site twice a month, in intervals ranging from 10 to 15 days, resulting in a total of 40 field trips, each representing a temporal window. The coldest months, June and July, in which the plant composition was more constant, and February were sampled just once. Each field trip lasted three to four days, with

observations on bee's flower visiting behavior and pollination mechanisms of flowers lasting one to two days. The following two days were spent by a single collector walking for 40 minutes in each plot in a sequence that was drawn by random. Each plot was sampled three times per day resulting in total of two hours/plot/day. The sequence of plot sampling was inverted in the second day such as different plots were visited in different times of the day. We collected bees interacting with the flowers with a net for further identification. *Apis mellifera*, *Trigona spinipes* and *Bombus* species which were easily identified during flight were not collected, instead we just counted them as they were observed in flowers.

Plant-visitor interactions

During observations of bee-flower interactions we registered the following aspects: (1) the flower resources explored; (2) the contact, if any, to anthers and stigma; (3) the activation of flower mechanisms in morphological specialized flowers, if any (*e.g.* exposure of reproductive organs of keel flowers); (4) the congruence between flower morphology and bee behavior (*e.g.* if buzz-pollinated flowers and anther vibration by its visitors, and long corolla flowers visited through its entrance, not by lateral holes). Based on those observations we classified bees as *pollinators* when, at least in half of their visits in a given plant species, they were observed visiting flowers as expected by flower morphology and contacting the anthers and stigma. On the other hand, bees were classified as *robbers* when they did not contact the flower's anthers and stigma and in all visits they did not behave as expected by flower morphology. In this paper we use "robber" as a generic term for all flower larcenists, thus including all kinds of robbers and thieves (for a review of the terminology of floral larceny see Irwin et al. 2010). The function of a bee (if either robber or pollinator) was recorded for each plant species, so a bee could be classified as pollinator for one plant species and as robber for another. Information about bee species, function and the plants they interact with are available as appendix (Supplementary material Appendix 1-2).

Flower traits

The following floral traits were registered in the field: flower type, color, symmetry and available resources offered. These traits were selected because together they reflect pollination syndromes and preferences of flower visitors. Flower types were classified into seven categories by their morphology and pollination mechanism following Faegri and Pijl (1979),

Endress (1994), Westerkamp (1997) and Westerkamp and Claßen-Bockhoff (2007): dish (open flowers), brush, keel, gullet-funnel (flowers open enough that a bee can enter with at least their heads), tube (flowers with long corolla tubes which only mouthparts of visitors enters), bilabiate (flowers with dorsiventral organization and dorsal pollen transfer) and buzz (flowers with poricidal anthers pollinated by buzzing). Since most of the studied bees have mouthparts longer than 3 mm, we included all flowers with corolla length shorter than 3 mm in the dish type (once all bees were capable to reach the resource, even if it was not an open flower). Flowers with corolla length of 3 mm or longer were included in the tube type. Corolla length was determined based on measurements taken from at least five flowers from different plants using a caliper. Flower color was classified into seven classes, based on the main visual spectra: blue; greenish-white (not pure white colors, with greenish, yellowish, or brownish white tonalities); pink; purple; red; white; and yellow. Flower symmetry was classified in three classes (Neal et al., 1998): asymmetric, bilateral (monosymmetric, zygomorphy) and radial (actinomorphic, more than 2 plans of symmetry). Flower resource was determined either by direct observation and, for some cases, literature was consulted (Renner e Feil, 1993; Freitas e Sazima, 2003; Filho et al., 2011; Chauveau et al., 2012; Maia, 2013). As “resources available” we meant those that could be reached by visitors without damaging flowers, during visits congruent to flower morphology. This was considered different from “resource collected” which corresponds to the resource collected or used by the visitor (*e.g.*: if one bee robs pollen from the hidden anthers of a nectar-flower, we classified the resource available as nectar, and the resource collected as pollen).

Matrix construction

Since we intend to study niche partitioning between robbers and pollinators, for different temporal windows and in the resources used when both bee functions are in activity, we discarded data from field trips were robbery was not observed. The observed interactions were used to construct a single bipartite quantitative plant-visitor interaction matrix with bee species in the rows and plant species in the columns. The bees from this bee-plant web were then merged by their function, either robber or pollinators, to build a **function-plant network** (**FNP**). In this matrix, bee species were merged based only on bee function, so we had a matrix with columns corresponding to plant species, two rows, based on the bee’s function, and cell values representing the number of visits observed between corresponding plant and function.

Finally we made five matrices using flower traits instead of the plant species. In such matrices the rows corresponded to kind of interaction (robbery or pollination) and columns corresponded to one of the categories of each flower traits described in the previous section. In this way, we had five function-flower trait webs: **function-color**, **function-flower type**, **function-symmetry**, **function-resources available** and **function-resources collected**. We also made a bee-plant and a function-plant matrix for each temporal window, resulting in a total of 33 networks of each kind.

Analysis of network properties and niche partitioning

To understand if robbers and pollinators were using different flower traits and which traits were used by each kind of visitor, first we carried a χ^2 test for each of the function-flower trait webs. The χ^2 test evaluated whether the distribution of visits of each kind was related to the flower trait. Then we summarized network structure of function-flower trait webs using network and species-level specialization indexes (H_2' and d' respectively), partner diversity and species degree (k). Significance levels of H_2', d' and partner diversity were obtained by comparison with null networks generated using '*r2dtable*' method in the 'bipartite' package in R software (R Development Core Team, 2014) with 1000 replicates. We used the specialization indexes H_2' and d' to describe the niche complementarity and specialization on different partner association respectively (Blüthgen et al., 2006; Blüthgen, 2010) by each bee function for each flower trait. Higher values of H_2' can be interpreted as higher complementarity (or exclusiveness) in the use of different states of flower traits by the visitors of each function. We calculated the d' index for robbers and pollinatiors, and a large d' means that visitors belonging to that category are found on less visited flower traits and small if the number of visits on that trait is predicted by neutrality. Since we have just two functions, we can interpret d' also as a measure of niche partitioning, since it is related to H_2' and larger values would be reached when both functions show different patterns of flower trait exploiment. The partner diversity index corresponds to the Shannon diversity of the interactions for a given species. As for the diversity index, it is a function of the equitability of distribution of number of visits among states of a flower trait and trait richness. The degree usually indicates the number of species of the opposite level interacting with one node of the network. In our case the degree of visit type indicates the number of states encompassed by both robbers and pollinators in each flower trait.

Since specialization properties between robbers and pollinators might be better evaluated for each temporal window sampled (each field trip), we compared *d'*, *k* and partner diversity of robbers and pollinators from each temporal window by paired *t*-test. When data did not meet homogeneity and normality assumptions, we carried the proper data transformations.

Network structure prediction – temporal overlap models

To evaluate if phenology and flower traits could predict the function-plant network structure, we constructed interaction-probability models for each flower trait and two based on temporal overlap. The first step was construct two temporal matrices based on monthly occurrences. We thus had one temporal matrix for plants ($\mathbf{O_{tp}}$) and one for bees ($\mathbf{O_{tb}}$) with species in rows, months in columns and cell values of "0" and "1" indicating absence and presence of a given species in a given month. We also constructed a temporal matrix based on function ($\mathbf{O_{tf}}$) where we have bee's function in rows. In order to do this, we summed the column values of the bees' temporal matrix ($\mathbf{O_{tb}}$) for each function. Thus we obtained a matrix where cell values represent the number of species of either robbers or pollinators for each month. Note that bees observed as robbers and pollinators were computed twice since they could interact in both ways. With these matrices, we constructed the two temporal overlap models. For the first temporal overlap model (**T1**), we considered that each plant species could be robbed by any robber, even if it was not observed visiting a given plant. We did this based on the idea that any robber can use resources from any flower since robbery might not demand any morphological match between the robber and the flower (although some morphological traits of bees can actually affect its function, as showed by Amaral-Neto et al., 2015). For this model, plants blooming in months with more robbers or with more pollinators had a higher probability to be robbed or pollinated, respectively. We used matrix multiplication to calculate temporal overlap between plants and functions as described in Vázquez et al. (2009), where $\mathbf{T1= O_{tp}\ O_{tf}'}$. For the second temporal overlap model (**T2**) we considered that plants could be robbed by any of its visitors. For this we first calculated the probability of a plant to be visited by robbers or pollinators based on the proportion of the observed robbed plant species. So, if we had 113 plants species and 27 were robbed the probability of a plant to be robbed was 27/113, and the complementary fraction (86/113) represents the probability of a plant to be visited by a pollinator. Then, we calculated the amount of temporal overlap between a plant species and all

of its visitors, not regarding bee's function. We did this by matrix multiplication of temporal matrices of plant and bee species(**$T = O_{tp} O_{tb}'$**, as in Vázquez et al., 2009) and summing cell values of columns afterwards. To finally obtain the second temporal overlap model (**T2**), the probability of a given plant to be visited by each function due to temporal overlap was obtained by multiplying the amount of temporal overlap of this plant to be visited and the probability to be robbed. The same process was carried out to find the probability of each plant to be pollinated. All probability matrices were normalized to sum one.

Network structure prediction – trait complementarity models

Under the assumption that interactions were determined solely by the preferences of visitors for some specific categories of each trait, we calculated the interaction probability between each kind of visit, robbery or pollination, and each category of flower trait. This was interpreted as a measure of trait complementarity (*e.g.* the probability of robbery at red flowers). In order to do that we used the number of visits of each function/flower trait matrix and transformed them in probabilities. Then, based on the flower traits of each plant species, we assigned the obtained probabilities to each plant (*e.g.* a plant with yellow keel flowers was assigned probabilities due to yellow flower and keel type visitation). When more than one plant species had the same trait category, the probability was divided by the number of species sharing that characteristic, in such a way that all plants with the same trait had the same chance of being visited. Based on that, we constructed models using flower color (**C**), flower type (**F**), symmetry (**S**) and resources available (**R**). "Resources collected" category was not included in this analysis since it is not a flower trait but depends on the behavior of the robber. Combined models of two and three flower traits were made combining these single-trait probability matrices by means of their element-wise product, and then normalizing to sum one. We also used the temporal models (T1 and T2) and combined traits and temporal models to create a total of 14 two-trait, 17 three-trait and two five-trait models. Lastly, we formulated a null model (**NULL**), in which all pairwise interactions probabilities between the kind of visit *F* and plants *P* were equal 1/*FP*.

Test of models

To evaluate if interaction probabilities derived from temporal overlap and function-plant trait complementarity were able to predict the observed plant/bee network proprieties, we

used a randomization algorithm implemented in R software by Vázquez et al. (2009) modified in order to give us the values of H_2' and d' for robbers and pollinators. The randomization algorithm generated 1000 random quantitative networks where the total number of interactions originally observed in the function-plant matrix was assigned according to the probability matrices defined by our 39 models, and the constraint that each species received at least one interaction.

We calculated H_2' and d' for robbers and pollinator for each random network, creating an expected distribution for these metrics against which we compared the observed values for the combined function-plant web. The observed values that fall within the 95% confidence interval of the generated networks provide evidence that the biological mechanisms included in our models were enough to predict the structural properties similar to the observed network.

In addition to evaluating structural network properties, we used those models to predict the observed pairwise interaction frequencies. The predictive ability of each model was estimated by the Akaike's information criterion (AIC) for each model (details in Vázquez et al. 2009). To compare the relative fit of competing models, we calculated ΔAIC values as the difference between the AIC generated by the observed function/plant and the observed network and each alternative model. We performed all calculations in R ver. 3.1.0 using the *bipartite* v 2.4 statistical packages (Dormann et al., 2008), and functions provided by Vázquez et al. (2009; Supplementary material).

Results

Interaction and plant morphology description

We documented 10,053 visits distributed among 113 plant and 200 bee species. We observed 27 plant species robbed by 32 bee species. Two of these 32 bee species exhibited only robbing behavior: *Chalepogenus unicolor* (Apinae – Tapinotaspidini) in *Angelonia integerrima* (Plantaginaceae) and *Paroxystoglossa brachycera* (Halictinae – Augochlorini) in *Peltaea edouardii* (Malvaceae). Six plant species were only visited by robbers: *Agarista pulchella* (Ericaceae), *Campomanesia adamantina* (Myrtaceae), *Gelasine coerulea* (Iridaceae), *Hibiscus* sp. (Malvaceae), *Miconia hyemalis* (Melastomataceae) and Myrtaceae sp. 3 (Myrtaceae).

The more common flower traits were: white (30), yellow (28) and purple (30) colors; tubular (48) and dish (28) flower types; radial symmetry (86) and; flowers where both pollen and nectar were available (62) (see Supplementary material Appendix 2). Pollinators and robbers were observed using all plant traits categories.

Network analyses

The number of visits in each function varied significantly with all flower traits (flower type, χ^2 = 3397.32, DF= 6, p<0.001; resource collected, χ^2 = 1530.90, DF=3, p<0.001, resource available, χ^2 = 986.16, DF= 4, p<0.001; color, χ^2 = 780.14, DF= 6 p<0.001 and; symmetry, χ^2 =168.72, DF=2 p<0.001).

Most function-flower trait webs showed low, but significant specialization (Table 2). The function-resources collected network was the most specialized network followed by function-flower type, function-available resources, function-color and function-symmetry networks.

Robbers were more specialized (*d'*) than pollinators for all flower trait networks. The highest values were observed for flower type and resources collected (Table 2). Robbers had higher partner diversity for flower type, available resources and symmetry networks while pollinators had higher partner diversity at resources collected and color networks (Table 2). Finally, since robbers and pollinators were using all traits, they had the same degree which is equal to the number of categories for that trait (Table 2).

Temporal aspects of FNP network

When each field trip (temporal window) was taken into account, the mean specialization of FNP networks was high (mean=0.79, sd=0.23). Robbers were more specialized ($t_{(32)}$=-4.27; p<0.001), with less interactions (degree - $t_{(32)}$=13.56;p<0.0001) and had lower partner diversity ($t_{(32)}$=9.73; p<0.0001) than pollinators. The proportion of available plant species shared between pollinators and robbers each month is low, with many months (ten) with distinct compartmentalization, in which no plant species were shared by the different bee behaviors (Fig.1).

Do traits predict function-plant networks?

No interaction probability model was able to accurately predict H_2', pollinators and robbers *d'* (Fig. 2). The model including only flower type (F) was the best, generating distribution

values closest to the observed metrics, followed by the three parameters models including flower type, available resources and time (FRT1 and FRT2), although the last ones had a high variation around the mean. Generally, the worst models were those including flower symmetry as one of the parameters, and the worst models were both temporal overlap models, the null model (NULL) and that including only symmetry (S).

The color (C) model provided the best fit to the observed species pairwise interaction frequencies in the likelihood analysis, although it had an extremely large ΔAIC of 23,456.82. The second best model was the color-symmetry one (CS) which has a difference of only 47,311 from the C model, indicating that both can be considered equally good models (see Fig 2 for full likelihood results). The worst models (with higher ΔAIC values) were NULL, S, CFRST1 and CFRST2. However even the best models pointed by AIC still had poor scores when compared to the observed FNP matrix fitted to itself, indicating that much remained unexplained.

Discussion

Are robbers and pollinators sharing resources?

Although pollinators and robbers use the same flower traits, our results show that each function concentrates their visits in at least one different trait category, which was expressed by the values of H_2' and d', and can alo be observed in Fig. 4. This means that robbers and pollinators show some degree of niche complementarity instead of a strong niche overlap. This is especially true for function-flower type and function-resource collected networks, which were the most specialized (larger H_2' and d' values). Those traits also showed higher influence in the distribution of visits by each function. Flower type network specialization was due to partitioning by robbers concentrating their visits on bilabiate, brush and buzz-pollinated flowers while pollinators were more frequent on dish and keel flowers. Resource collected network specialization was mostly due to niche partitioning between robbers concentrating their visits on pollen collection while pollinators were mostly collecting just nectar or pollen and nectar on the same flower (Fig. 4).

Niche partitioning and partner diversity in flower-type and resource-collected networks were highly influenced by the large number of visits by honeybees (*Apis mellifera*), which were concentrated on dish and tube-flowered Asteraceae, where they collected nectar and pollen. This specialization of pollinators due to the high number of visits by honeybees contributed to

network specialization and robbers *d'*, since robbers concentrated their visits on different flower-type categories (higher niche partitioning). If the number of visits by honeybees were not so high, probably the pollinators would show more equally distributed visits and the degree of specialization of functions and of the network itself would decrease. Preliminary tests on rarefaction of *A. mellifera* visits showed tendencies in agreement with this hypothesis.

On the other hand, robber specialization was mainly due to the high visitation on bilabiate and buzz-pollinated flowers, where pollen and oil are collected. Due to their morphology, these flowers are pollinated only by few species with morphological and behavioral matching. The low visitation rate by pollinators may result in high resource availability, which can be exploited by robbers that can bypass flower morphological restrictions. Some studies showed a high frequency of robbers in restrictive nectar flowers (Irwin e Brody, 1998; Maloof e Inouye, 2000; Irwin et al., 2010; Wang et al., 2013; Zhang et al., 2014). Robbers usually are pointed as competitors of pollinators usually by depleting this resource from visited flowers (Roubik, 1982; Irwin et al., 2010; Wang et al., 2013). In the present study, however, instead of a strong competition due to niche overlap, robbers concentrates their visits in some morphological restrictive flowers (bilabiate, buzz-pollinated) where the rate of pollinator visitation is low.

Although available resources and color networks showed low H_2' values when compared to flower type and resources collected, they were also significant. Most trait categories are used by pollinators and robbers with similar proportion and the amount of niche partitioning detected in these networks is mainly due to specialization of robbers in oil, pollen and in red flowers. Robbers were much more frequent than pollinators in the observed oil flowers, in particular for *Angelonia integerrima*. Robbing by the frequent and small-bodied tapinotaspidine bees in the large oil flowers of Plantaginaceae was also reported by Martins et al. (2013), who also observed that visitation rate of pollinators on those flowers is low. In our study most interactions of robbers are due to pollen robbery, contrasting with the tendency pointed by most studies where nectar larceny is more common (Maloof e Inouye, 2000; Irwin et al., 2010; Wang et al., 2013). Robbers were observed robbing pollen from nectar, oil and pollen-nectar flowers, resulting in the observed high specialization on collected-resource network but a lower specialization on the network of available resource. Finally, red flowers are related to bird pollination and the color can be considered a “private channel” for hummingbirds (Faegri e Pijl,

1979; Chittka e Waser, 1997; Lunau et al., 2011). Otherwise, intense robbery by bees is common on red flowers (Roubik, 1982; Chittka e Waser, 1997). Since we are only observing bees, pollinators were rarely seen on those flowers. The exceptions were two species of Megachilinae bees (*Epanthidium nectarinioides* and *Megachile iheringi*) on *Collaea speciosa* (Fabaceae) which were observed making legitimate visits and possibly acting as pollinators.

Niche complementarity between pollinators and robbers become even more evident in temporal networks. The lower degree and partner diversity and higher *d'* of robbers in temporal networks indicates that these bees concentrate the visits within each temporal window in a few species. For many temporal windows pollinators and robbers did not share any plant species, a pattern that was not detected when pooled networks were analyzed. When doing so, shared plant species correspond only to a small proportion of the available plant species (Fig.1), resulting in the high specialization of FNP networks. It is possible that shared species correspond also to those most abundant. If this is true, resources would be so abundant that pollinators and robbers are not competing for it. Besides that, pollinators can forage on many plant species from where they could obtain resources other than the robbed ones. In such way, perhaps robbers are visiting plants after or before the peak of pollinators' visits or they are visiting very abundant species which are rarely visited by pollinators, thus the competition effects due to niche overlap are low. Nonetheless, this hypothesis needs to be tested by more detailed observations on temporal dynamics of the pollinator-robber-plant systems.

Do traits predict function-plant networks?

As for specialization, flower type trait and models including this trait corresponded to the best models to predict FNP metrics. However, the best models to predict network properties were not the best ones to predict pairwise species interactions, a conclusion also reached by some recent works (Vázquez et al., 2009; Olito e Fox, 2014; Vizentin-Bugoni et al., 2014). The better prediction of network properties by flower type model can be attributed to the small difference between the number of visits of robbers on bilabiate and buzz-pollinated flowers and keel and tube flowers (Fig. 1). This results in similar probabilities for those flower type states to be visited by robbers. In this case, network properties can be simulated by assigning interactions to any of the pairwise interactions with similar probabilities. However, this does not necessarily reproduce the pairs of interactive plant species and bee function of the real network.

Color model, otherwise, assigns distinct probabilities for each state, and thus generates more different probabilities to pairwise interactions. By doing this, the properties of the FNP network are harder to predict by random distribution of visits among different colors (properties are reached only by assigning interactions to very specific pairs). Otherwise, the pairwise interactions are more likely to be assigned since each function-color interaction has distinct probabilities (so interactions are less prone to be assigned to other pairs with similar probabilities). This explanation is similar to that given by Vizentin-Bugoni et al. (2014) to the modest importance of abundance in plant-hummingbird networks. When traits are combined a similar situation is achieved, with many pairwise interactions having the same occurrence probabilities, as in our FRT1 and FET2 models. Eklöf et al. (2013) suggest that single traits can sometimes be enough to predict much of the network structure, and the usage of many traits would increase redundancy. So models combining many traits may more easily predict network structure, due to the overlap of probabilities, but may still be poor in explaining pairwise interactions. This may explain why in other studies the best predictor models of network proprieties were those combining few traits although they still failed to predict pairwise interactions (Vázquez et al., 2009; Olito e Fox, 2014; Vizentin-Bugoni et al., 2014). In face of those arguments, we suggest that the relation between proportion of similar probabilities in a model and its power of predicting network properties, as well as pairwise interactions, should be dealt in future studies.

Although some network metrics such as connectance and nestedness seems to be relatively easy to predict (Fox, 2006; Olito e Fox, 2014), H_2' and d' seem to be more complicated. When the network to be predicted has lower H_2' and d' values, models with overlap probabilities should have good results due to easiness of generating many niche overlaps. Otherwise our FNP network has high H_2' and d' values, and the increase in redundancy generated by similar probabilities of pairs make the achievement of niche complementarity by null models a hard task. That would explain why we have no models capable of predicting those proprieties for our FNP network. While other metrics depends more on the individual distribution of interactions of each species, simulation of higher values of H_2' and d' further requires a specific pattern of distribution of visits of all species in order to create a niche complementarity, turning those metrics harder to reach by null models.

The difficulty in predicting interactions in FNP networks by traits may be due to the fact that different rules are driving pollinators and robbers towards plants. Several studies show that pollinators follow a series of rules when visiting plants, with preferences and choices by visitors taking into account many flower traits (Gegear e Laverty, 2001; Gegear, 2005; Cakmak et al., 2009; Junker et al., 2013). In many studies, morphological matching between flowers and their visitors are among the most important factors to predict network structure (Olito e Fox, 2014; Vizentin-Bugoni et al., 2014). However, morphological matching is not very useful for robbers, since there is no need of a morphological match between these bees and their visited flowers. Perhaps robbers are making their choices based mainly on higher energy uptake as suggested by Irwin et al. (2010). If so, including flower abundance in the models should give us better results. Future studies on robber species could focus on their flower choices in order to understand why visitors behave as robbers.

As far as we know, the present study is the first focusing on niche partitioning of robbers and pollinators in a network context. Due to the specialization of robbers, both by concentrating their visits on flowers with traits less used by pollinators and by most of the time sharing few or no plant species with them, we can say that robbers and pollinators are not strong competitors within the community context. Features leading to their choices, however, still need to be studied.

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Tables

Table 1. Model descriptions.

Model/Matrix abbreviation	Description
FNP	Observed interactions between function of bees and plant species – Matrix we want to predict
T1	Temporal overlap where robbers can rob from any plant
T2	Temporal overlap where plants can be robbed only by their observed robbers
C	Visits are determined solely by flower color
F	Visits are determined solely by flower morphology
R	Visits are determined solely by resources available
S	Visits are determined solely by flower symmetry
CFRST1*	Visits are determined by mixed probabilities from flower trait models and temporal overlap T1
CFRST2*	Visits are determined by mixed probabilities from flower trait models and temporal overlap T2
NULL	All interactions have the same probability

*Combined probability models are calculated as the element-wise product between single trait probability models. The other combined probability matrices are abbreviated by coupling the correspondent single trait probability model abbreviations. (*e.g.* CS – Color-symmetry model).

Table 2. Network and species level indexes. Higher values for each trait are shown in bold.

Flower trait	X^2 (DF)	H_2'	Function	d'	Partner diversity	K
Flower type	3397.32* (6)	0.42*	Robber	**0.46***	**1.66***	7
			Pollinator	0.23*	1.33*	7
Resources collected	1530.90* (3)	0.57*	Robber	**0.32***	0.83*	4
			Pollinator	0.10*	**1.03***	4
Available resources	986.16* (4)	0.19*	Robber	**0.11***	**1.35***	4
			Pollinator	0.09*	1.04*	4
Color	780.14* (6)	0.17*	Robber	**0.16***	1.39*	7
			Pollinator	0.05*	**1.51***	7
Symmetry	168.72* (2)	0.04*	Robber	**0.04***	**0.92***	3
			Pollinator	0.01*	0.61*	3

*p-values < 0.0001

Figures

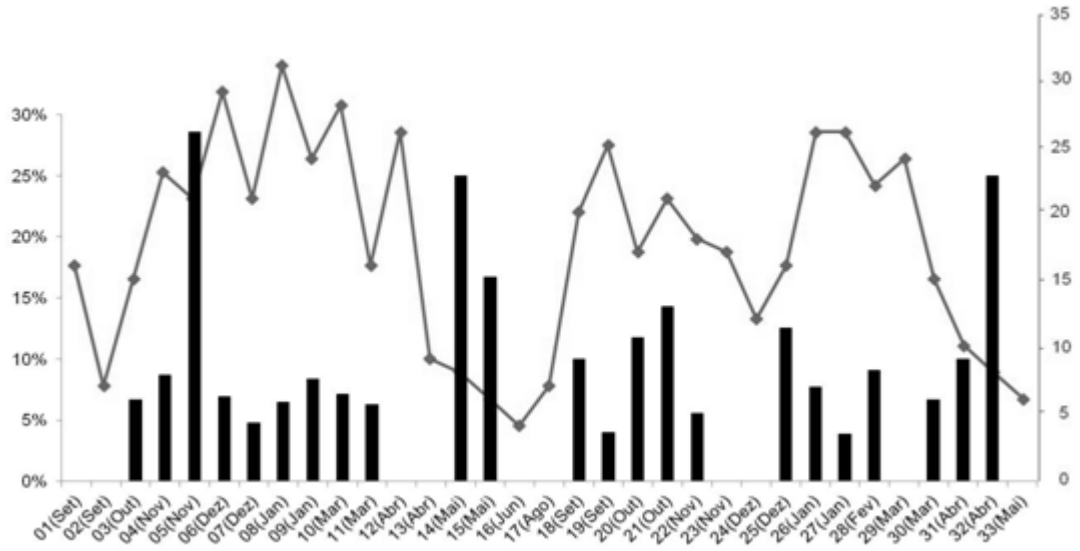

Figure 1. Proportion of the available plant species shared by pollinators and robbers in each of the 33 temporal windows and number of available plant species (grey line). Note that in some temporal windows, no plant was shared (*e.g.* 13abr). Numbers preceding month's names abbreviations indicate the order of temporal windows.

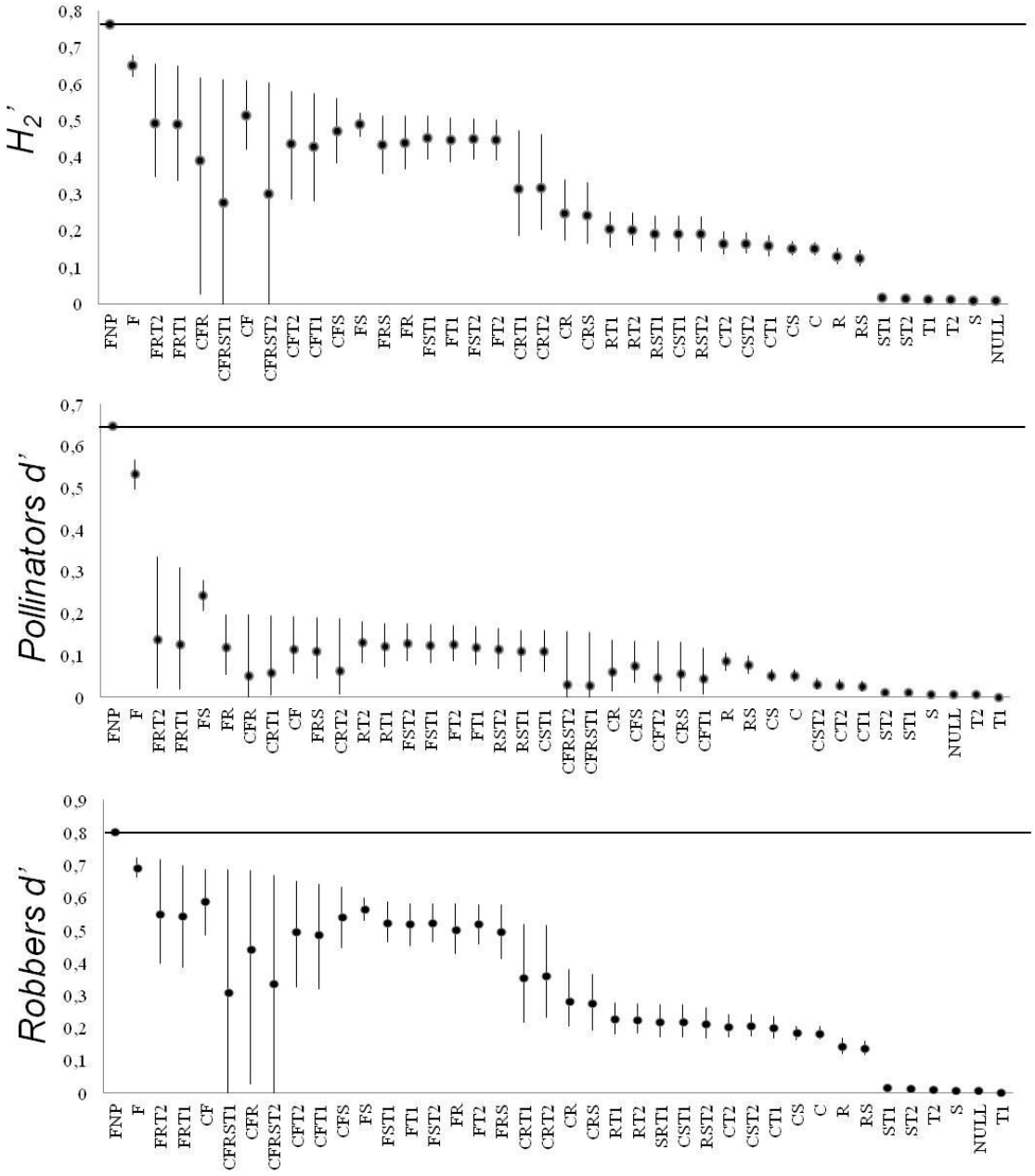

Figure 2. Values of aggregate network statistics (circles, mean; bar, 95% confidence interval) produced by 1000 randomizations of probabilistic matrices in relation to the observed value of the function-plant network (FNP, horizontal line). The probabilistic matrices are based on two distinct temporal models (**T1** and **T2**), flower type (**F**), available resource (**R**), color (**C**) and symmetry (**S**) or combinations of them. **NULL** is a null model in which all interactions had the same probability.

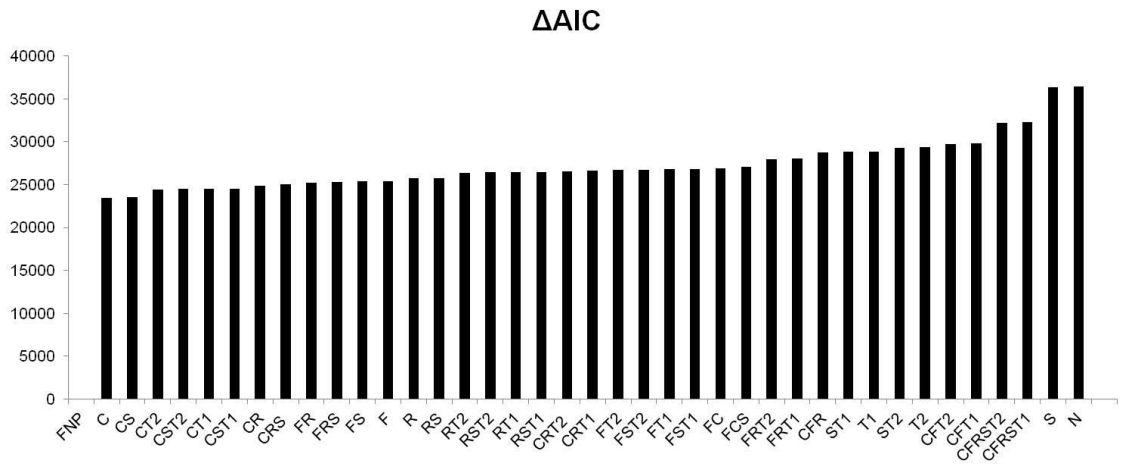

Figure 3. Comparison of ΔAIC values of the 39 probabilistic models with the value obtained by fitting observed function-plant (FNP) network to itself. The probabilistic matrices were based on two distinct temporal models (**T1** and **T2**), flower type (**F**), available resource (**R**), color (**C**) and symmetry (**S**) or combinations of them. **NULL** is a null model in which all interactions had the same probability. The models are arranged in decreasing fit, from up to down, with shorter bars representing better models.

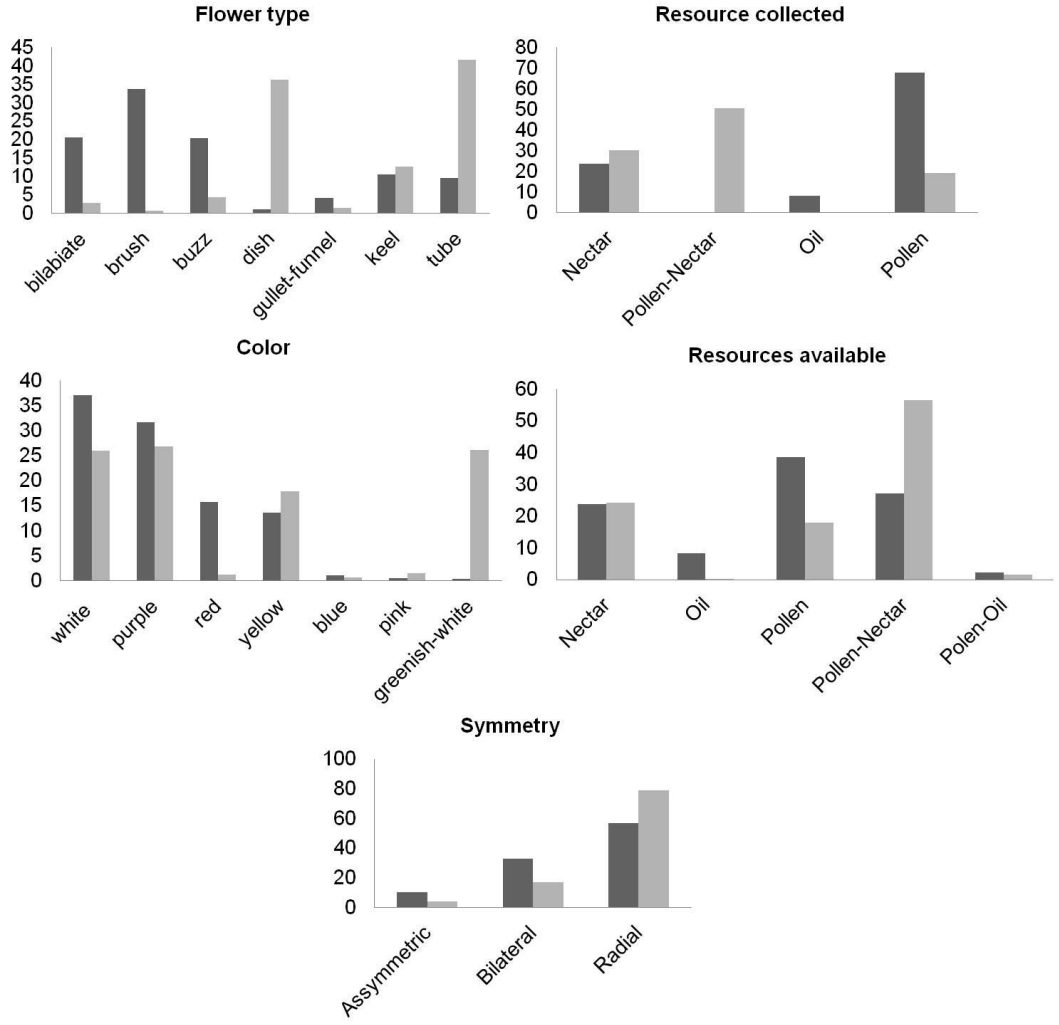

Figure 4. Proportional number of visits by each function on each flower trait. Light grey bars represent the visits of pollinators and darker bars those of robbers.

Supplementary material

Appendix 1. List of studied plant species and their respective flower traits. An asterisk after the species name indicates that it was visited only by robbers. Sp = Specie number; R = radial; B = bilateral; A = asymmetric; N = nectar; P = pollen; O = Oil; PN = pollen and nectar; PO = pollen and oil.

Species number	Family and Plant species	Color	Symmetry	Flower type	Available resource
	Amaranthaceae				
1	*Pfaffia tuberosa* (Spreng.) Hicken	White	R	Dish	N
	Apiaceae				
2	*Eryngium elegans* Cham.&Schlecht.	White	R	Dish	N
3	*Eryngium junceum* Cham.	Purple	R	Dish	N
	Arecaceae				
4	*Allagoptera campestris* (Mart.) Kuntze	Greenish-white	R	Dish	P
5	*Butia microspadix* Burret.	Greenish-white	R	Dish	PN
	Asteraceae				
6	*Aspilia foliacea* (Spreng.) Baker	Yellow	R	Dish	PN
7	*Aspilia montevidensis* (Spreng.) Kuntze	Yellow	R	Dish	PN
8	Asteraceae sp.4	Yellow	R	Tube	PN
9	*Baccharis articulata* (Lam.) Persoon	White	R	Tube	PN
10	*Baccharis crispa* Spreng.	White	R	Tube	PN
11	*Baccharis dracucunlifolia* DC.	White	R	Tube	PN
12	*Baccharis linearifolia* (Lam.) Pers.	White	R	Tube	PN
13	*Baccharis myricaefolia* DC.	White	R	Tube	PN
14	*Baccharis trilobata* A.S.Oliveira & Marchiori	White	R	Tube	PN
15	*Baccharis uncinella* DC.	White	R	Tube	PN
16	*Baccharis verticilata*	White	R	Tube	PN
17	*Calea cuneifolia* DC.	Yellow	R	Dish	PN
18	*Calea hispida* (DC.) Bak.	Yellow	R	Tube	PN
19	*Calea longifolia* Gardner	Yellow	R	Tube	PN
20	*Calea monocephala* Dusén	Yellow	R	Tube	PN
21	*Calea platylepis* Sch.Bip. ex Baker	Yellow	R	Tube	PN
22	*Chromolaena congesta* (Hook. & Arn.) R.M.King & H.Rob.	Purple	R	Tube	PN
23	*Chromolaena laevigata* (Lam.) R.M.King & H.Rob.	Purple	R	Tube	PN
24	*Chrysolaena lithospermifolia* (Lam.) R.M.King & H.Rob.	Purple	R	Tube	PN
25	*Disynaphia caliculata* (Hook. & Arn.) R.M.King & H.Rob.	Purple	R	Tube	PN
26	*Elephantopus mollis* Kunth	Purple	R	Tube	PN
27	*Eupatorium* aff. *laevigatum*	Purple	R	Tube	PN
28	*Eupatorium multifidum* DC.	White	R	Tube	PN
29	*Gochnatia polymorpha* (Less.) Cabrera	Greenish-white	R	Dish	PN
30	*Grazielia intermedia* (DC.) R.M.King & H.Rob.	White	R	Tube	PN
31	*Heterocondylus reitzii* R.M.King & H.Rob.	Purple	R	Tube	PN
32	*Hypochaeris radicata* L.	Yellow	R	Tube	PN

33	*Isostigma speciosum* Less.	Red	R	Tube	PN
34	*Lessingianthus argenteus* (Less.) H.Rob.	Purple	R	Tube	PN
35	*Lessingianthus grandiflorus* Less.	Purple	R	Dish	PN
36	*Lessingianthus polyphyllus* (Sch.Bip. ex Baker) H.Rob.	Purple	R	Tube	PN
37	*Lessingianthus simplex* (Less.) H.Rob.	Purple	R	Tube	PN
38	*Mikania hirsutissima* DC.	Greenish-white	R	Tube	PN
39	*Piptocarpha axillaris* (Less.) Baker	White	R	Dish	PN
40	*Pterocaulon angustifolium* DC.	Greenish-white	R	Dish	P
41	*Senecio brasiliensis* (Spreng.) Less.	Yellow	R	Tube	PN
42	*Senecio oleosus* Vell.	Yellow	R	Tube	PN
43	*Solidago chilensis* Meyen	Yellow	R	Tube	PN
44	*Stenocephalum megapotamicum* (Spreng.) Sch.Bip.	Purple	B	Tube	PN
45	*Trichocline speciosa* Less.	Yellow	R	Tube	PN
46	*Verbesina sordences* DC.	Yellow	R	Tube	PN
47	*Vernonanthura nudiflora* (Less.) H.Rob.	Purple	R	Tube	PN
48	*Vernonanthura oligolepis* (Sch.Bip.) H.Rob.	Purple	R	Tube	PN
49	*Vittetia orbiculata* (DC.) R.M.King & H.Rob	Purple	R	Tube	PN
	Bignoniaceae				
50	*Jacaranda oxyphylla* Cham.	Purple	B	Bilabiate	N
	Boraginaceae				
51	*Moritzia dusenii* I.M.Johnst.	Blue	R	Tube	PN
	Clethraceae				
52	*Clethra scabra* Pers.	White	R	Dish	PN
	Convolvulaceae				
53	*Ipomoea maurandioides* Meisn.	Purple	R	Gullet-funnel	PN
	Ericaceae				
54	*Agarista pulchella* [*] Cham. ex G.Don	Red	R	Tube	PN
	Euphorbiaceae				
55	*Croton antisyphiliticus* Mart.	Greenish-white	R	Dish	PN
56	*Croton heterodoxus* Baill.	White	R	Dish	PN
	Fabaceae				
57	*Chamaecrista desvauxii* (Collad.) Killip	Yellow	A	Buzz	P
58	*Chamaecrista punctata* (Vogel) H.S.Irwin & Barneby	Yellow	A	Buzz	P
59	*Collaea speciosa* (Loisel.) DC.	Red	B	Keel	N
60	*Crotalaria micans* Link	Yellow	B	Keel	N
61	*Eriosema glabrum* Mart. ex Benth.	Yellow	B	Keel	N
62	*Eriosema heterophylum* Benth.	Yellow	B	Keel	N
63	*Galactia neesii* DC.	Purple	B	Keel	N
64	*Macroptilium prostratum* (Benth.) Urb.	Yellow	A	Keel	N
65	*Pomaria stipularis* (Vogel) B.B.Simpson & G.P.Lewis	Yellow	A	Buzz	P
	Gesneriaceae				

66	*Sinningia allagophylla* (Mart.) Wiehler	Red	B	Bilabiate	N
	Iridaceae				
67	*Gelasine coerulea* [*](Vell.) Ravenna	Blue	R	Gullet-funnel	PO
68	*Sisyrhinchium micranthum* Cav.	Red	R	Dish	PO
69	*Sisyrinchium brasiliense* (Ravenna) Ravenna	Yellow	R	Dish	PO
70	*Sisyrinchium restioides* Spreng.	Yellow	R	Dish	PO
71	*Sisyrinchium vaginatum* Spreng	Yellow	R	Dish	PO
	Lamiaceae				
72	*Peltodon rugosus* Tolm.	White	B	Keel	N
73	*Rhabdocaulon gracile* (Benth.) Epling	White	B	Bilabiate	N
74	*Rhabdocaulon lavanduloides* (Benth.) Epling	Purple	B	Bilabiate	N
75	*Salvia aliciae* E.P.Santos	Purple	B	Bilabiate	N
76	*Salvia lachnostachys* Benth.	Purple	B	Bilabiate	N
77	*Hyptis apertiflora* Epling	Purple	R	Tube	PN
	Lobeliaceae				
78	*Lobelia camporum* Pohl	White	B	Bilabiate	N
	Lythraceae				
79	*Cuphea glutinosa* Cham. & Schltdl.	White	B	Bilabiate	N
80	*Cuphea linarioides* Cham. & Schltdl.	Pink	B	Bilabiate	N
	Malpighiaceae				
81	*Aspicarpa pulchella* (Griseb. ex Mart.) O'Donell & Lourteig	Yellow	B	Dish	PO
82	*Byrsonima intermedia* A. Juss.	Yellow	B	Dish	PO
83	*Byrsonima psilandra* Griseb.	Yellow	B	Dish	PO
	Malvaceae				
84	*Hibiscus sp.* [*]	Red	R	Gullet-funnel	N
85	*Peltaea edouardii* (Hochr.) Krapov. & Cristóbal	Pink	R	Gullet-funnel	N
86	*Sida macrodon* DC.	Red	R	Dish	P
87	*Sida* sp.	Yellow	R	Dish	P
	Melastomataceae				
88	*Acisanthera alsinaefolia* (Mart. & Schrank ex DC.) Triana	Purple	R	Buzz	P
89	*Leandra simplicicaulis* (Naudin) Cogn.	White	R	Buzz	P
90	*Miconia theizans* (Bonpl.) Cogn.	White	R	Tube	PN
91	*Miconia hyemalis*[*] A.St.-Hil. & Naudin	Greenish-white Naudinhyemalis	R	Tube	N
92	*Tibouchina gracilis* (Bonpl.) Cogn	Purple	R	Buzz	P
93	*Tibouchina martialis* Cogn.	Purple	R	Buzz	P
	Mimosaceae				
94	*Mimosa dolens* var. *acerba* (Benth.) Barneby	Pink	R	Brush	PN
95	*Mimosa dolens* var. *rudis* (Benth.) Barneby	Pink	R	Brush	PN
	Myrtaceae				
96	*Campomanesia adamantina* [*] (Cambess.) O.Berg.	White	R	Brush	P
97	Myrtaceae sp2	White	R	Brush	PN

98	Myrtaceae sp3*	White	R	Brush	PN
	Passifloraceae				
99	*Piriqueta taubatensis* (Urb.) Arbo	White	R	Gullet-funnel	N
	Plantaginaceae				
100	*Angelonia integerrima* Spreng,	Purple	B	Bilabiate	O
	Rhamnaceae				
101	*Rhamnus sphaerosperma* Sw.	Greenish-white	R	Dish	PN
	Rubiacae				
102	*Borreria poaya* (A.St.-Hil.) DC.	Purple	R	Gullet-funnel	PN
103	*Borreria verticillata* (L.) G. Mey	White	R	Dish	PN
104	*Borreria paranaensis* E.L.Cabral & Bacigalupo	White	R	Tube	PN
105	*Galianthe elegans* E.L.Cabral	White	R	Tube	PN
	Scrophulariaceae				
106	*Buddleja elegans* Cham. & Schltdl.	Greenish-white	R	Tube	N
	Solanaceae				
107	*Calibrachoa linoides* (Sendtn.) Wijsman	Pink	B	Bilabiate	N
108	*Solanum aculeatissimum* Jacq.	Greenish-white	R	Buzz	P
109	*Solanum pseudocapsicum* L.	White	R	Buzz	P
110	*Solanum reitzii* L.B.Sm. & Downs	White	R	Buzz	P
	Verbenaceae				
111	*Lippia hirta* (Cham.) Schauer	Purple	B	Tube	N
112	*Lippia lupulina* Cham.	Pink	B	Tube	N
113	*Verbena hirta* Spreng.	Purple	R	Tube	N

Appendix 2. List of studied bee species and the plants where they were observed. The numbers in the column "Plant species" correspond to species numbers (Sp) in the Appendix 1. An asterisk after the number of plant species indicates robbery interactions.

Bee species	Plant species*
ANDRENINAE	
Calliopsini	
Callonychium petuniae Cure & Wittmann, 1990	*56, 85*, 86,107*
Oxaeini	
Oxaea flavescens Klug, 1807	*47*
Protandrenini	
Anthrenoides sp.	*30, 32, 41, 55, 58, 75, 76, 107*
Psaenythia annulata Gerstaecker, 1868	*2, 3, 10, 18, 26, 32, 41, 44, 49, 50*, 56, 64, 70, 72, 76, 85*, 94, 95*, 92, 102, 103, 104, 105, 107, 113*
Psaenythia bergii Holmberg, 1884	6, 18, 26, 71, 76
Psaenythia collaris Schrottky, 1906	*105*
Psaenythia quadrifasciata Friese, 1908	*2, 18, 22, 25, 27, 36, 44, 57, 95*
Psaenythia sp.2	*58, 110*
Psaenythia sp.3	*105*
Rhophitulus reticulatus (Schlindwein & Moure, 1998)	*56, 112*
Rhophitulus sp.1	10, 12
APINAE	
Anthophorini	
Anthophora (Mystacanthophora) paranensis Holmberg, 1903	*47, 58, 77, 73, 75, 76, 102, 113*
Apini	
Apis mellifera Linnaeus, 1758	*2, 3, 4, 5, 6, 8, 9, 10, 11, 14, 15, 16, 17, 18, 21, 22, 23, 24, 25, 27, 28, 29, 30, 31, 32, 33, 34, 36, 38, 39, 40, 41, 42, 44, 47, 48, 51, 52, 54*, 55, 56, 71, 72, 75, 76, 77, 90*, 91*, 94, 95, 95*, 97, 98*, 95, 101, 102, 103, 104, 105, 111, 46, 113*
Bombini	
Bombus (Fervidobombus) pauloensis Friese, 1913	8, 18, 22, 23, 24, 27, 31, 32, 34, 35, 36, 44, 47, 48, 50, 51, 54*, 57, 58, 64, 65, 67, 71, 72, 73, 75, 76, 77, 78, 79, 87, 92, 94, 95, 101, 102, 103, 105, 110, 112, 46, 113
Bombus brasiliensis Lepeletier, 1836	*50, 58*
Bombus morio (Swederus, 1787)	8, 18, 21, 24, 27, 31, 34, 35, 36, 41, 44, 47, 48, 50, 51, 58, 65, 72, 73, 75, 76, 77, 88, 92, 102, 103, 110, 112, 46, 113
Centridini	
Centris (Centris) nitens Lepeletier, 1841	*18, 58*
Centris (Centris) varia (Erichson, 1849)	*24, 36, 50, 58, 93, 105*
Centris (Hemisiela) tarsata Smith, 1874	*58, 64, 76, 113*

Trigona spinipes (Fabricius, 1793)	*1, 4, 5, 10, 15, 21, 24, 30, 32, 35, 36, 38, 41, 42, 43, 44, 50*, 51, 53*, 54*, 56, 57*, 58*, 59*, 61*, 67*, 68, 69, 71, 73*, 75*, 77, 78*, 84*, 87, 92*, 95, 95*, 97, 99, 101, 102*, 103, 46*
Nomadini	
Doeringiella (Orfilana) cingillata Moure, 1954	*41*
Thalestria spinosa (Fabricius, 1804)	*33*
Osirini	
Osiris sp.1	*80, 102*
Parepeolus niger Roig-Alsina, 1989	*113*
Tapinitaspidini	
Tapinotaspoides serraticornis (Friese, 1899)	*18, 22, 24, 27, 34, 35, 36, 44, 47, 77, 80, 85, 87, 102, 107, 113*
Caenonomada labrata Zanella, 2002	*113*
Arhysoceble dichroopoda Moure, 1948	*80, 107*
Arhysoceble picta (Friese, 1899)	*113*
Arhysoceble sp.1	8, 32, 64, 79, 82, 85, 100*, 102
Arhysoceble xanthopoda Moure, 1948	*64, 79, 81, 100*, 102, 113,*
Chalepogenus unicolor Roig-Alsina, 1999	*100**
Lanthanomelissa aff. *clementis*	8
Lanthanomelissa betinae Urban, 1995	*32, 51, 79, 80, 102*
Lophopedia nigrispinis (Vachal, 1909)	*24, 36, 82*, 107, 111*
Monoeca campestris Aguiar, 2012	24
Paratetrapedia punctata Aguiar & Melo, 2011	*24, 42, 44, 47, 64, 71, 79, 80, 82, 83, 85, 102*
Xanthopedia iheringii (Friese,1899)	*77, 82**
Xylocopini	
Ceratina (*Ceratinula*) sp.2	6, 15, 16, 42, 86, 103
Ceratina (Crewella) rupestris Holmberg, 1884	*18, 41, 42, 51*
Ceratina (Crewella) sp.2	17, 18, 24, 25, 26, 35, 36, 37, 42, 44, 46, 47, 50*, 51, 53, 56, 71, 73, 102, 107, 112, 113
Ceratina (Crewella) sp.7	*51, 53, 113*
Ceratina (Crewella) sp.8	*32, 44*
Ceratina (Rhysoceratina) sp.1	6, 8, 18, 20, 24, 32, 35, 36, 37, 42, 44, 51, 56, 71, 72, 102, 105, 112, 113
Ceratina (Rhysoceratina) sp.3	6, 8, 10, 32, 34, 36, 51, 53, 56, 61*, 63*, 72, 102, 105, 112, 113
Ceratina (Rhysoceratina) sp.4	8, 41, 76, 113
Ceratina (Rhysoceratina) sp.5	*51, 63**
Xylocopa (Nanoxylocopa) ciliata Burmeister, 1876	*33, 34, 36, 41, 48, 58, 63, 66, 72, 75, 76, 102, 105, 112*
Xylocopa (Neoxylocopa) augusti Lepeletier, 1841	*50*, 54*, 58, 110*
Xylocopa (Neoxylocopa) frontalis (Olivier, 1789)	*58, 60, 93*
Xylocopa (Schonnherria) macrops Lepeletier, 1841	*58*
COLLETINAE	

CAPÍTULO II

Como os pilhadores afetam a estrutura de uma rede de interações abelha-planta?*

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How do robbers affect the structure of a bee-plant network?

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Abstract

Network studies on flower-visitor community usually assume that all links are between pollinators and their plants. However, some animals, especially bees, sometimes gather flower resources without providing pollination services. The effect of those floral larcenists was already explored from the plant perspective and flower-visitor guild in many studies but it remains unexplored from a community network perspective. We collected data for two years in a grassland community of bee-plant visitors, in southern Brazil. The proportion of robbery interactions and changes in network topology due to exclusion of larcenists for each temporal window was recorded. We found that a small proportion (<10%) of interactions correspond to robbery, although a significant smaller number of species (both plant and bees), lower nestedness and bee specialization (*d'*) is present in networks without robbers. Compartmentalization, network specialization (H_2') and plant properties remain unchanged. Nonetheless, even for unchanged properties we found variable effects of robbery interactions related to the position of those interactions in the network. Despite small changes caused by robbery interactions, the role of those within the network structure results in variable consequences at temporal-window aggregated-network statistics which are important to ecological interpretations and for understanding of community functioning. We further discuss those consequences and highlight the importance to identify the robbery interactions within the so called 'mutualistic plant-pollinator' networks.

Introduction

Plant-animal interactions within a community have been studied as a complex web of links between the plants and the animals visiting them. Those plant-animal mutualistic networks assume that all represented interactions are beneficial for both partners, thus representing an arena on which evolutionary processes occur (Bascompte e Jordano, 2007). In plant-pollinator networks, for example, the term 'pollinator' is a generic designation for all kinds of flower visitors (Elberling e Olesen, 1999; Olesen et al., 2008). However, not all interactions between plants and flower visitors are pollination interactions, and those mutualistic networks are passive to 'cheaters' – flower-visiting animals which deplet flower resources but do not provide pollination services (Genini et al., 2010).

While floral larcenists, animals are usually referred as "robbers", when they pierce flowers to obtain the resources, and "thieves" when they get pollen or nectar without damaging flower tissues (Inouye, 1980; Irwin et al., 2010). The effect of floral larceny in plant reproduction ranges from negative to neutral or even positive effects (Maloof e Inouye, 2000; Irwin et al., 2010). Besides that, the presence of robbers can cause changes in the behavior of other flower visitors. The main effect of robbers is to lower the amount of resources available for legitimate visitors (Stout et al., 2000; Maloof, 2001). This may cause visitors to spend less time on flowers, to avoid robbed flowers or to fly longer distances between visits (Maloof, 2001; Richardson, 2004; Mayer et al., 2014; Zhang et al., 2014), which can have indirect effects on plant reproduction and gene flow. Although it's clear that floral larceny has consequences to plant reproduction and flower-visitor behavior, these studies were done focusing in a single plant species. Thus, the effect of flower robbers and thieves in the community, where there are many flower species available at the same time, has not been so far explored.

Robbery is more common on flowers with concealed nectar (Irwin et al., 2010), and studies have shown that large proportions of flowers within a population may be robbed (Irwin e Brody, 1998; Stout et al., 2000; Richardson, 2004). Not only flowers with concealed nectar are likely to be robbed, but brush and buzz-pollinated pollen flowers are also visited by many insects which deplete pollen from anthers without providing pollination services (Nascimento e Del-Klaro, 2007; Del-Klaro et al., 2009). It is possible, then, that many interactions in flower

visitation webs are due to larcenists, and should not be computed as plant-pollinator interactions, as already pointed out by others authors (Irwin et al., 2001; Genini et al., 2010). Irwin and co-authors (2001) proposed some effects that robbers can have in community structure. For example, they might contribute to the long-term persistence and play a role in the stability of these systems by displacing visitation niche of pollinators to plants previously less visited, in order to avoid competition, increasing reproductive success of the new plant. In an interaction web of many plant species, pollinators can avoid foraging on the robbed less-rewarding species and so increase the visitation rate in other more profitable plants (Irwin et al., 2001). This difference in realized niche of flower visitors can be reflected in network structure. However those authors were also aware that the effects have been so far not experimentally explored. A network approach by Genini and co-authors (2010) have compared webs with and without robbers and found that floral larcenists increase network modularity, and are more dispersed within a module than acting as connectors between modules. Their study, however, focused on species within two plant families, and not on the whole plant-visitor community.

In the present study we take a further step and investigate the effects of robbers within a community by comparing networks of bee-plant visitators with and without robbery interactions looking for changes in their properties. We also observed the proportion of visits due to flower larcenists and further discuss the implications of including non-pollinator interactions in network studies. Based on our results of first chapter, we expect that robbery represents just a small proportion of visits in the flower visitor community and, since both guilds, robbers and flower visitors, do not share many of the available resources, the removal of larcenists from the network would have no strong effects in the network structure. We also expect that robbers acts as very specialized bees (in the temporal context) which interacts with very connected plants, thus not causing strong impacts for network.

Material and Methods

Study system and sampling methods

We studied flower visitation by bees in natural grasslands at the State Park of Vila Velha, Ponta Grossa, Paraná, Brazil for two years, from August 2011 to August 2013. The study site is located around the coordinates 25°14'13"S and 49°59'58"W, at 900-910 m above sea

level (for further details see Gonçalves et al. 2009) and was subdivided into four contiguous plots of 50 x 50m each for sampling purposes. We visited the study site twice a month, in intervals ranging from 10 to 15 days, resulting in a total of 40 field trips, each representing a temporal window. The coldest months, June and July, in which the plant composition was more constant and February were sampled just once. Each field trip lasted three to four days, with observations on bee's flower visiting behavior and pollination mechanisms of flowers lasting one to two days. The following two days were spent by a single collector walking for 40 minutes in each plot in a sequence that was drawn by random; each plot was sampled three times per day. The order of plot visits was inverted in the second day such as different plots were visited in different times of the day. We collected bees interacting with the flowers with a net for further identification. *Apis mellifera*, *Trigona spinipes* and *Bombus* species which were easily identified during flight were not collected, instead we just counted them as they were observed in flowers.

Plant-visitor interactions

During observations of bee-flower interactions we registered the following aspects: (1) the flower resources explored; (2) the contact, if any, to anthers and stigma; (3) the activation of flower mechanisms in morphological specialized flowers, if any (*e.g.* exposure of reproductive organs of keel flowers); (4) the congruence between flower morphology and bee behavior (*e.g.* if buzz-pollinated flowers and anther vibration by its visitors, and long corolla flowers visited through its entrance, not by lateral holes). Based on those observations we classified bees as *pollinators* when, at least in half of their visits in a given plant species, they were observed visiting flowers as expected by flower morphology and contacting the anthers and stigma. On the other hand, bees were classified as *robbers* when they did not contact the flower's anthers and stigma and in all visits they did not behave as expected by flower morphology. In this study we use "robber" as a generic term for all flower larcenists, thus including all kinds of robbers and thieves (for a review of the terminology of floral larceny see Irwin et al. 2010). The function of a bee (if either robber or pollinator) was recorded for each plant species, so a bee could be classified as pollinator for one plant species and as robber for another. Information about bee species, function and the plants they interact with are available as appendix (Supplementary material Appendix 1-2).

Dataset and network properties analyses

Since we intend to compare the network properties of webs with and without robbers, we discarded data from field trips were robbery was not observed. The observed interactions of each field trip were used to construct a total of 33 quantitative plant-visitor interaction matrix, from now on called **visitor-plant network** (**VP**), where robbers are included. From each visitor-plant web we excluded all interactions characterized as robbery, resulting in 33 **pollinator-plant networks (PP)**, each of them corresponding to the same temporal window of a VP. We then calculated the proportion of links (L) and individual interactions (N) due to robbery. 'Links' are pairs of interacting species of each level (bee and plant), with their observed frequency not taken into consideration. The number of individual interactions is the number of visits recorded between any bee-plant species pair. To understand the effect of robbers in network properties we compared by paired *t*-tests the following network indexes: specialization (H_2'), number of compartments (*nComp*), weighted nestedness (*WNODF*), number of plants and bee species, and for plants and bees: mean specialization (*d'*), mean weighted degree (*wk* to differ from the normal degree *k*) and mean number of shared partners (*shp*) in VP and PP networks. When data did not meet homogeneity and normality assumptions, we carried out the proper data transformations. We performed all calculations in R ver. 3.1.0 using the *bipartite* v 2.4 statistical packages (Dormann et al., 2008) and *vegan* (Oksanen et al., 2013) statistical packages.

We chose these metrics because they are especially sensitive to changes in niche complementarity. For example, we used the specialization indexes H_2' and *d'* to describe the niche complementarity and specialization on different partner association respectively (Blüthgen et al., 2006; Blüthgen, 2010). In this case, if robbers and pollinators are visiting the same plants, we expect higher values of H_2' and *d'* when they are excluded from networks. We also used the number of compartments, which are sub-sets of the web which are not connected (through either higher or lower trophic level) to another compartment (Dormann et al., 2008). This is much more restrictive than modularity since compartments are not formed when there is any connection between modules. So, if robbers are connectors, we expect that their exclusion results in networks more compartimentalized. WNODF is a nestedness metric for quantitative networks based on overlap and decreasing fill of interactions in the matrix (Almeida-Neto et al., 2008; Almeida-Neto e Ulrich, 2011). Two basic properties are required for a matrix to have the

maximum degree of nestedness according to this metric: (1) complete overlap of the interactions from less-filled columns and rows (more specialized species) with those found in more-filled rows and columns (more generalist species); (2) decreasing marginal totals between all pairs of columns and all pairs of rows (Almeida-Neto et al., 2008; Almeida-Neto e Ulrich, 2011). Since the bee genus more commonly described as robbers, such as bumble bees (Bombus sp.), stingless bees (*Trigona* spp.) and *Apis mellifera* (Irwin et al., 2010), usually make many interactions with high number of visits (generalists), we expect a lower nestedness when they are removed. This expected lower nestedness would be due to removal of the higer marginal total of rows (corresponding the interactions of the robber) which would probably decrease the overlap of interactions between more-filled rows with the less-filled rows.

The degree indicates the number of species of the opposite level interacting with one node of the network. We used the mean weighted index, which corresponds to the sum of links for each species, averaged over all species in that level, taking into account the number of observations for a given species. The weighted version was used so that the index value is based on the degree of more common species, rather than rare or few observed species, which have lower degrees (based on Bersier et al., 2002).

. The number of shared partners counts the number of species in the other level that a given pair of species interact with, *e.g.* for bees it yields the mean number of plants shared by a pair of flower visitor species. For both degree and mean number of shared partners we predict a decrease when robbers are excluded since robbers are expected to be visiting the same plants as the pollinators are.

Results

We documented 10,053 visits distributed among 113 plant species and 200 bee species. The proportion of links and individual interactions due to robbery ranged from 1.8% to 35.3% and from 0.4% to 67.7%, respectively in each temporal window, and usually were lower than 10% (Fig 1).

We observed 27 plant species robbed by 32 bee species. Two of these 32 bee species were exclusively robbers: *Chalepogenus unicolor* (Apinae – Tapinotaspidini) in *Angelonia integerrima* (Plantaginaceae) and *Paroxystoglossa brachycera* (Halictinae – Augochlorini) in *Peltaea edouardii* (Malvaceae). Six plant species were only visited by robbers:

Agarista pulchella (Ericaceae), *Campomanesia adamantina* (Myrtaceae), *Gelasine coerulea* (Iridaceae), *Hibiscus* sp. (Malvaceae), *Miconia hyemalis* (Melastomataceae) and Myrtaceae sp. 3 (Myrtaceae). For many months pollinators and robbers did not visit the same plant species (low niche overlap) and when doing so, only a small proportion of available plant species were shared (for further details see chapter 1, fig.1).

The exclusion of robbery resulted in a lower WNODF, as well as lower d'_{bees} and wk_{bees} (Table 1). Most of the network properties evaluated were not modified by the exclusion of robbery interactions from the network (Table 1).

Although not showing significant differences, niche partitioning was high for networks with and without robbers (mean $H_2'_{PV} = 0.69$, sd = 0.13 *and* mean $H_2'_{PP} = 0.67$, sd = 0.15 respectively). For many temporal windows (19 out of 33) the number of plants and bee species and the number of compartments were not affected by the exclusion of robbery interactions (Table 2). We observed, however, a temporal fluctuation in the other months with eight temporal windows that exhibited more compartments and six with fewer compartments after exclusion of robbery (Table 2).

Discussion

In the studied networks only a small proportion of observed interactions and pairwise links were due to robbery. We found, however, that the proportion of robbery varied seasonally, with months exhibiting higher or lower numbers of robbery interactions. Studies focusing on single plant species show that floral larceny intensity varies greatly among species (e.g. from 59% in *Corydalis caseana* to 96% at a wild population of *Linaria vulgaris*), but usually high rates of robbery (more than 50%) are commonly observed (Maloof e Inouye, 2000; Maloof, 2001). Some of these studies also found that the proportion of robbed flowers varies in time and space (Stout et al., 2000; Richardson, 2004; Zhang et al., 2014). However these proportions are based on the number of flowers robbed from a single population, not the number of visits by robbers. Genini and co-authors (2010) showed that the number of links due to robbery is three times higher in Bignoniaceae than Malpighiaceae visitation networks, and that those links correspond to a large proportion of the Bignoniaceae interactions. If we have such differences between single species or between two plant families, what could we expected in a community context?

In a community context robbers are more likely to specialize temporally in plants with specific traits and tend to concentrate their visits in a few plant species when small temporal frames instead of the whole-year network are observed (Amaral-Neto et al. first chapter). The small average proportion of robbery links are due to this specialization. The number of individual interactions tends to follow the same tendency as the number of links, but for some months the number of individual visits by robbers is much higher (Fig 1). The seasonal variation of robbery rates is associated with the abundance and diversity of available plant species (Fig 1), and so, of their flower traits. If pollinators change their behavior in the presence of robbers by avoiding plundered flowers and flying longer distances (Maloof, 2001; Richardson, 2004; Mayer et al., 2014; Zhang et al., 2014), in a community context these visitors are probably changing their visits to other less robbed plant species. When the abundance of flower species and traits are low, pollinators would be more prone to leave the community, and a higher proportion of robbery is observed (Fig 1). Even if the number of plant species is low, with flowers morphologically simple without physical restrictions, such as those with poricidal anthers or long corolla tubes, bees are less likely to obtain resources by robbery, becoming legitimate pollinators. This is the case, for example, of interactions at July where the most abundant plant were *Baccharis* crispa, *Senecio oleosus* (Asteraceae) and *Rhamnus sphaerosperma* (Rhamnaceae), which have simple open flowers with both polen and nectar, thus all visitors were considered pollinators. Since most robbers are social bees, thus having workers foraging yearlong, seasonal variation in the proportion of robbery is less likely to be due to variable abundance of the larcenists. The causes of seasonal variation in levels of robbery and the relation between the abundance and diversity of plant species and flower traits is, however, an open field for further investigations.

The exclusion of robbery did not modify niche complementarity (H_2') and affected only d'_{bees}. The similar values of H_2' and d'_{plant} with and without robbery indicates that for many networks those interactions were not strong redundant with pollination interactions, neither the same plants were being used. If robbery and pollination interactions had strong overlap, the exclusion of the first would increase the H_2' by reduced redundancy of interactions (Blüthgen et al., 2006; Blüthgen, 2010). In addition, robbery comprises just a small proportion of interactions, usually less than 10%. So the general pattern of observed niche partitioning (H_2' value) is more

due to how pollinators share the resources. In fact since robbers temporally shared few plant species with pollinators (Amaral-Neto et al. first chapter), it would be expected that their exclusion would not affect niche partitioning between legitimate visitors. Consequently, niche partitioning and higher overall robber specialization (Amaral-Neto; first chapter, table 4) also explain the smaller *d'* and *wk* of bees when larceny interactions are removed (specialized species were excluded, and some of their links). Plant network properties were not affected by exclusion of robbery interactions probably because robbed plants showed the same species level properties than pollinated ones, with similar degree and exhibiting similar specialization. Fig 2 shows that exclusively robbed plants have low degree and interact with few bees, as many of the pollinated plants do. That would explain why the mean values of aggregate statistics did not show significant differences when robbed plants were excluded from networks.

Although exclusion of robbery interactions did not affect *nComp* and nestedness, temporal variation of these properties were observed. For compartimentalization, temporal changes can be interpreted as follows: (1) When more compartments are observed after exclusion of robbery (eight networks), it means that robbers are uniting compartments (Fig 2A); (2) When fewer compartments are observed (six networks), it indicates that some compartments are composed exclusivelly by robbery interactions (Fig 2B), and finally; (3) For months in which robbed plants, their robbers and their legitimate pollinators are inside a single compartment (19 networks), *nComp* is not affected (Fig 2C). We found that most interactions of robbery are dispersed within compartments of pollination interactions, with fewer occurrences of robbery between compartments and even less compartments composed solely by robbery interactions. A similar pattern has been detected in the visitation network for Bignoniaceae (Genini et al., 2010). When pollinators and robbers share the same plants, robbery interactions comprise a subset of the pollinator's niche, generating a nested pattern. So, when robbers were excluded it results in smaller nestedness. Differently from Gennini and co-authors (2010), who found that cheater links contribute only to modularity, we found an effect on nestedness.

The nested pattern has been implied in the generation of a more stable association between mutualistic communities making them more resilient to perturbations (Bascompte et al., 2003, 2006; Memmott et al., 2004; Thébault e Fontaine, 2009). This resilience is due to the fact that nestedness implies that generalist bees interact with specialized plants and vice versa.

Therefore plants that lose a specialist pollinator can rely on more generalist partners. On the other hand, if well-connected bees are lost, nestedness yields a linear loss of plant species, since only the very specialized species loses their pollinators (Memmott et al., 2004). However, if robbery interactions usually have detrimental effects on plant reproduction (Irwin et al., 2010), the increase of nestedness due to cheaters does not necessarily represents a more resilient network, since loss of the well-connected pollinators could imply that plants would rely on robbers for their reproduction. Previous work showed that nested networks are more fragile under preferential elimination of more connected species (Burgos et al., 2007), even so, the presence of cheaters would increase this fragility under that circumstance. Nestedness also is thought to enhance coexistence between species by lowering interspecific competition, which would allow a higher biodiversity (Memmott et al., 2004; Bastolla et al., 2009). In this case, increased nestedness in VP networks can explain the coexistence between robbers and pollinators within a community, allowing a higher species diversity although without increasing competition (Bastolla et al., 2009) and because robbed plants do not show strong dependency for robbers, and at the same time pollinators can obtain resources from other plants besides those under robbery.

In addition to nestedness, many mutualistic networks exhibit a compartmentalized structure where some groups of species (compartments or modules) are more tightly linked together, sharing few links with other groups (Olesen et al., 2007; Vázquez et al., 2009). Mutualistic networks are at the same time nested and modular, especially large, low connected ones (Olesen et al., 2007; Fortuna et al., 2010). Even for our small networks (<50 species) we found strong compartmentalization with a mean of four compartments, different from Olesen and co-authors (2007). Compartments are also supposed to increase stability in food-webs because disturbance effects are more restricted to compartments instead of the whole network structure but they have little influence on persistence in mutualistic networks (Olesen et al., 2007; Thébault e Fontaine, 2009; Stouffer e Bascompte, 2011). Compartments in plant-pollinator networks may also correspond to units where species within them are under more tight reciprocal selection, and therefore resulting in suites of features corresponding to the pollination syndromes (Olesen et al., 2007; Danieli-Silva et al., 2012).

Nevertheless, ecological interpretation of network properties and its consequences to species coexistence, conservation and evolution require some precautions (Olesen et al., 2007; Blüthgen, 2010; Blüthgen e Klein, 2011). For plant-visitation networks the biological content of compartments and identification of whether links represent pollination or robbery interactions have to be considered. For example, decrease of compartmentalization and niche partitioning due to loss of compartments formed only by robbery interactions would not represent impacts on the community of plant and pollinators in the sense of plant and animal reproduction and resource gathering. Plant-pollinator interactions may also be more compartmentalized or modular without robbers acting as connectors, what can lead to a tighter correspondence between compartments and modules to pollination syndromes and trait matching interactions. Compartments of robbers or mixed compartments of robbers and pollinators may also be evolutionary important. Larceny compartments may constitute an evolutionary arena in the direction of plant defenses against robbery and not towards a closer trait matching between plants and their visitors, as usually thought of mutualistic plant-visitor networks. Robbers can cause stronger selection on some flower traits than pollinators, sometimes depending on the degree that they affect plant reproduction (Irwin et al., 2004; Wang et al., 2013). In this sense identification of mixed compartments composed by both pollinators and robbers may provide good systems to study coexistence between both flower-visitor functions and the influence those interactions exert on the evolution of plants.

Network approach undoubtedly provides useful tools to study interacting species at community level. However a fully and proper interpretation of patterns can only be achieved by adding detailed biological information and knowledge of the processes leading to them. In the present study we observed that, despite the fact that robbery interactions have not drastically changed the structure of plant-visitor networks, the biological interpretation of patterns can be obscured by misinterpreting this link function. Previous works have alerted about the pitfalls to be avoided when interpreting network patterns (Blüthgen et al., 2008; Blüthgen e Klein, 2011). Here one of these pitfalls—overlook of robbers in the so called “mutualistic” plant-“pollinator” networks—has been investigated. We propose that further studies should try to closer investigate how robbers really affect network resilience and the degree of correspondence between compartments and pollination syndromes after exclusion of larceny interactions.

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Figures

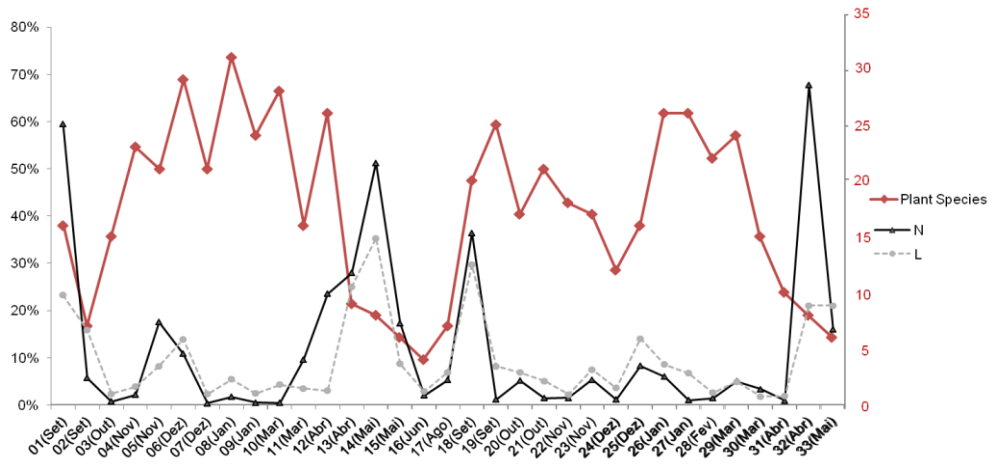

Figure 1. Proportion of the number of individual interactions (N) and links (L) due to robbery interactions and the number of plant species (red line), for each temporal window.

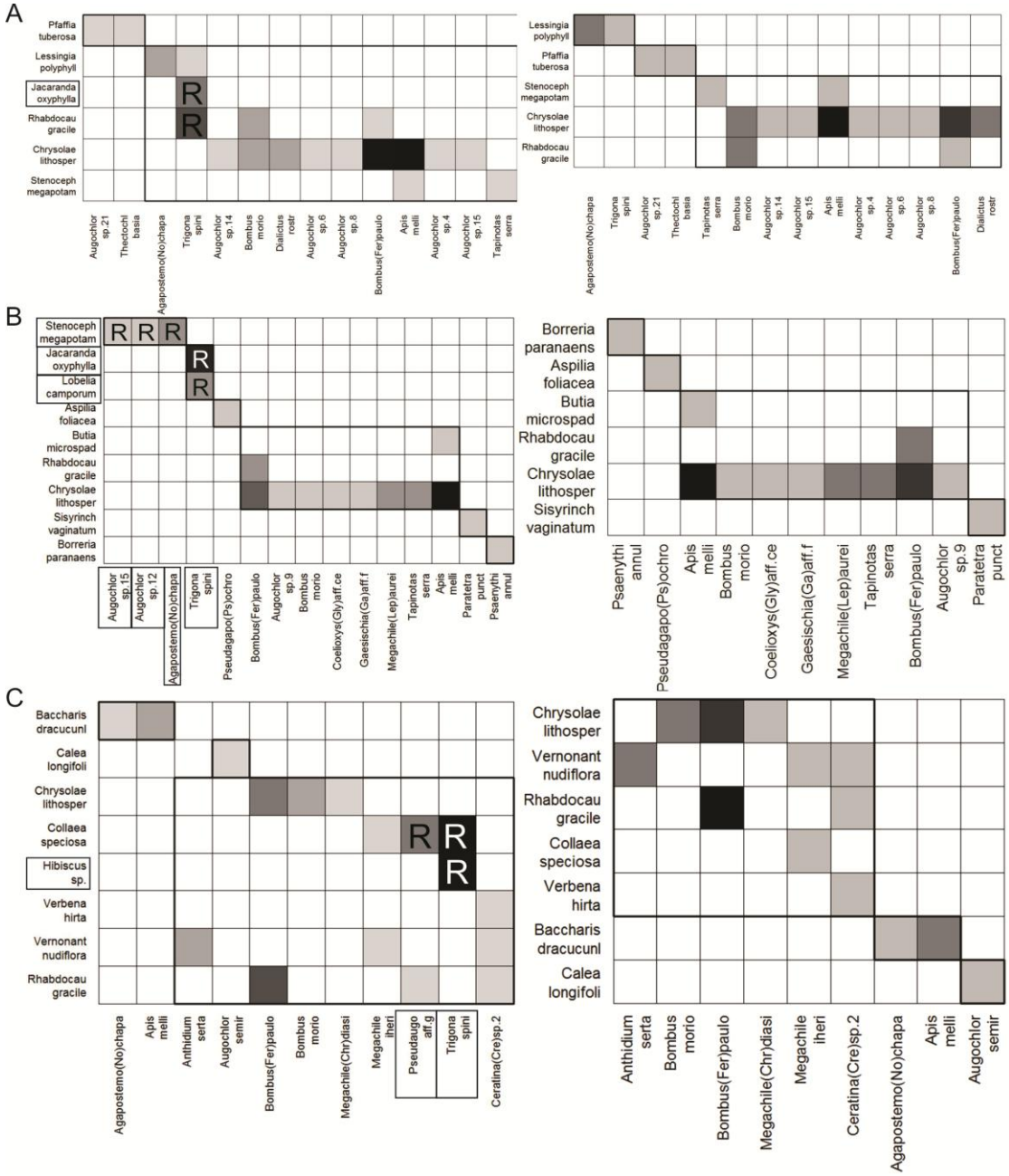

Figure 2. Compartments of some temporal windows with (left) and without (right) robbery interactions. The squares surround species that are not present at Plant Polinator networks. The "R" indicates robbery interactions. The level of grey within squares indicates the number of intercations, white means no interaction.

Tables

Table 1. Changes in network properties after the exclusion of robbery interactions. *nComp* number of compartments, WNODF weighted NODF (nestedness), *wk* weighted degree, *shp* number of shared partners.

Index	Effect of robbery exclusion	$t_{(32)}$	*p*-value
H_2'	Non significant	-1.07	p>0.05
nComp	Non significant	0.15	p>0.05
WNODF	Smaller	-2.57	p<0.05
Plant species	Smaller	-5.58	p<0.005
Bee species	Smaller	-5.31	p<0.005
d'_{bees}	Smaller	-2.31	p<0.05
d'_{plants}	Non significant	1.58	p>0.05
wk_{bees}	Smaller	-3.00	p<0.005
wk (plants)	Non significant	0.68	p>0.05
shp (bees)	Non significant	-0.31	p>0.05
shp (plants)	Non significant	-0.47	p>0.05

Table 2. Number of plant and bee species and compartments (*nComp*) for each field trip at PV (plant visitor) and PP (plant pollinators, robbery interactions excluded) networks.

Temporal	**Plants**		**Bees**		***nComp***	
window	PV	PP	PV	PP	PV	PP
01	16	10	18	18	5	5
02	7	6	13	12	6	6
03	15	15	23	23	4	5
04	23	23	41	41	2	2
05	21	20	48	47	2	3
06	29	24	36	32	5	3
07	21	21	16	16	2	3
08	31	29	44	41	8	6
09	24	24	45	45	5	6
10	28	28	42	41	2	2
11	16	15	26	26	3	4
12	26	25	35	35	9	9
13	9	6	15	11	6	4
14	8	6	9	7	5	5
15	6	5	14	14	2	3
16	4	3	15	15	1	1
17	7	6	24	22	1	1
18	20	16	30	26	5	9
19	25	23	45	44	3	3
20	17	16	49	49	2	2
21	21	20	53	52	4	4
22	18	17	49	49	6	6
23	17	16	40	39	4	5
24	12	11	21	21	8	8
25	16	15	34	30	7	6
26	26	25	35	32	5	5
27	26	23	34	31	3	1
28	22	22	32	31	4	4
29	24	22	32	31	7	6
30	15	15	30	29	2	2
31	10	10	27	26	1	1
32	8	7	11	9	3	3
33	6	4	10	9	1	1

CAPÍTULO III

Complementaridade fenotípica e interações proibidas são capazes de predizer as propriedades de uma rede de polinização abelha-planta? *

* Este capítulo foi organizado segundo as normas de publicação da revista OIKOS.

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Do trait complementarity and forbidden links predict the network properties of a bee - plant pollination web?

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Abstract

Trait matching is one of the hypotheses invoked to explain observed network patterns, because interactions between species are limited by phenotypic constraints. Studies on multiple determinants of network structure pointed out that trait matching is one of the factors, although not the most important, shaping the network. These previous studies used few phenotypic constraints and therefore might have underestimated the importance of trait matching. Here we evaluate the effect of multiple trait matching models on network structure. We identified phenology, complementarity traits (related to flower-visitor preferences) and forbidden link traits (which impose barriers to visitors) from a grassland bee-plant pollination network, in southern Brazil and evaluated their ability to predict network properties and pairwise interactions. Our results showed that complementarity trait models worked better than models using forbidden links due to the lack of barriers against bees in most plants. We also found that combinations of two traits are better predictors compared to when traits are used alone. Phenology alone performed poorly but strongly improves other models when combined. Finally we observed that the best models predicting pairwise interactions also performed well predicting network aggregated statistics. Our study suggests that use of at least two morphological constraints increases the prediction power of trait matching models probably due to a closer match with the identity of interactive species and thus, a better coupling between functional groups of bees and phenotypic traits involved in pairwise interactions. Our study supports the idea that trait matching may be more important in determining network structure than previously thought.

Introduction

Plants and animals interact in a pairwise fashion but when seen as a whole their interactions are embedded in larger community-wide networks. Considering interacting species as complex networks provides valuable insights about the whole system functioning, evolution and properties which cannot be achieved when pairs of interacting species are studied in isolation (Bascompte e Jordano, 2007; Blüthgen et al., 2007; Vázquez et al., 2009a; Blüthgen, 2010). Previous studies on mutualistic network revealed some pervasive patterns on their structural properties, such as compartimentalization, nestedness, and degree distribution (the number of species to which a given species is connected), with many species with few connections and a small proportion of species with many links (Bascompte et al., 2003; Jordano et al., 2003; Olesen et al., 2007; Vázquez et al., 2009a).

Two main hypotheses are used to explain the structure observed in mutualistic community networks: interaction neutrality and trait matching. Interaction neutrality hypothesis assumes that interactions between pair of species have no constraints, and thus they are assigned randomly with frequencies based on species abundance (Vázquez e Aizen, 2003; Santamaría e Rodriguez-Gironés, 2007; Krishna et al., 2008). Alternatively the trait matching hypothesis assumes that not all plants and animals in a community are able to interact due to phenotypic and spatio-temporal mismatching between interacting species, which may result in "forbidden links" (Jordano et al., 2003; Stang et al., 2006; Santamaría e Rodriguez-Gironés, 2007). Trait matching involves two possible mechanisms to the correspondence between traits of interacting species: trait complementarity and forbidden links. Complementarity traits do not impose direct barriers against bee visitation but it is related to coupling between bee's sensorial apparatus and preferences and attractive cues or resources exhibited by flowers, such as colors, nectar concentration, chemical cues and other flower signals (Santamaría e Rodriguez-Gironés, 2007; Blüthgen et al., 2008; Vázquez et al., 2009a). Otherwise, forbidden links consist in flower traits that can directly prevent a flower visitor from reaching the flower resources, and only those pollinators with specific set of traits can overcome those morphological constraints, *e.g.* flowers with long corolla tubes which demands long mouthparts or with poricidal anthers where flower visitors need the hability to buzz in order to reach the pollen (Santamaría e Rodriguez-Gironés, 2007; Blüthgen et al., 2008; Vázquez et al., 2009a). In addition to

morphological and behavioral traits, spatio-temporal distribution of species also determines if species are able to interact and may constitute forbidden links which influence network structure (Vázquez et al., 2009a; Maruyama et al., 2014).

Both neutrality and trait matching hypotheses do not exclude each other and some papers have evaluated the influence of multiple determinants in plant-visitor networks. Species abundance is usually pointed out as a major factor determining the structure of interaction network, although model prediction power increases when species traits are introduced (Krishna et al., 2008; Vázquez et al., 2009b; Olito e Fox, 2014). Recent studies focusing on interactions between hummingbirds and flowers showed, however, that morphology and spatio-temporal overlap between interacting species are more important than abundance to determine network structure and pairwise interactions (Maruyama et al., 2014; Vizentin-Bugoni et al., 2014). Despite some models which are able to predict network metrics, they failed to predict pairwise interactions of observed networks suggesting that other aspects of species biology not generally considered in network studies may be involved (Vázquez et al., 2009b; Olito e Fox, 2014). Perhaps the fact that these studies used only one morphological constraint to determine trait matching (Vázquez et al., 2009b; Olito e Fox, 2014; Vizentin-Bugoni et al., 2014) may preclude a proper understanding of the variables influencing some insect-plant interactions.

The influence of multiple traits on bee-plant interactions might be expected since their interactions have long influenced the evolution of both groups (Fenster et al., 2004; Mitchell et al., 2009). Interactions with plants lead to bee's morphological and behavioral adaptations for resource collecting and foraging patterns (Müller, 1996; Goulson, 1999; Niv et al., 2002; Krenn et al., 2005) while for plants we observe, for example, changes in mating systems and flower morphology associated to pollinator shift and pollinator behavior (Castellanos et al., 2004; Devaux et al., 2014) and changes towards avoidance of resource waste, such as development of poricidal anthers and keel flowers, which restrict the access to flower pollen and nectar (Buchmann 1983; Westerkamp 1997; Amaral-Neto, minor review).

The differences in flower morphology and how they could reflect pollinator type gave rise to the pollination syndrome concept, which implies that some suits of floral traits are associated with selective pressures exerted by specific pollinator groups (Faegri e Pijl, 1979; Fenster et al., 2004). Traditional view of pollination syndromes restricted the association of floral

traits to taxonomic groups of pollinators, such as bees, beetles and birds (Robertson, 1917; Pijl, 1961; Faegri e Pijl, 1979). These tight associations have been questioned since an apparent generalization of pollination systems is frequently observed, and flowers of a particular syndrome receive visits from diverse group of flower visitors (Waser et al., 1996; Johnson e Steiner, 2000). However, pollination syndromes do not imply the absence of others pollinators and may also be useful to predict secondary pollinators (Rosas-Guerrero et al., 2014), besides that, flower visitors can be grouped into functional groups, not regarding taxonomic proximity, which exhibits similar suit of traits and behave in similar ways on a flower and exert similar selective pressures (Fenster et al., 2004). For example interactions with long-tongued pollinators as diverse as moths, butterflies, and flies led to convergent evolution of long-spurred flowers in *Disa* species (Johnson et al., 1998). In *Mimulus luteus* and *Pestemon spp.* flower type also reflects adaptations towards its flower visitors, both bees and hummingbirds (Castellanos et al., 2004; Medel et al., 2007). In all these examples further comprehension of main functional groups of pollinators for each plant species is reached when other traits are added to flowers besides spur length and flower type, such as predominating colors, nectar concentration, corolla and nectar guide size (Johnson et al., 1998; Castellanos et al., 2004; Medel et al., 2007).

If both pollination syndromes and functional groups of pollinators are based on multiple traits, we believe that a study on the influence of trait matching on the network structure should include multiple traits in order to reflect flower and pollinator morphological and behavioral diversity. Facing this observation we investigated flower visitation behavior of bees in natural grassland vegetation in southern Brazil, trying to answer the following questions: (1) Is trait matching between bees and plants, including both forbidden links and trait complementarity, able to predict the observed network properties? (2) Are those mechanisms able to predict pairwise interactions?; and (3) If so, which one of them is the best predictor of network properties?

Material and Methods

Study system and sampling methods

We studied the flower visitation by bees at the State Park of Vila Velha, Ponta Grossa, Paraná, Brazil for two years, from August 2011 to August 2013. The sample site was covered by a natural grassland vegetation located around the coordinates 25°14'13"S and 49°59'58"W

and it is 900-910 m above sea level (for further details see Gonçalves et al. 2009). The study area was subdivided in four contiguous plots of 50 x 50m each for sampling porpoises. The study site was visited twice a month with intervals ranging from 10 to 15 days between field trips, resulting in a total of 40 field trips. The coldest months, June and July, in which the plant composition was more constant and February were sampled just once. Each field trip lasted three to four days. Observation of bee's flower visiting behavior and pollination mechanisms of flowers lasted one or two days. The following two days were spent with a single collector walking for 40 minutes in each plot in a randomly selected sequence; each plot was sampled three times per day. The order of plot visits was inverted in the second day such as different plots were visited in different times of the day. The bees interacting with the flowers were collected with a net for further identification, exception to those easily identified during flight. In this case they were just counted.

Plant-visitor interactions

During observations of bee-flower interactions we registered the following aspects: (1) the flower resources explored; (2) the contact, if any, to anthers and stigma; (3) the activation of flower mechanisms in morphological specialized flowers, if any (*e.g.* exposure of reproductive organs of keel flowers); (4) the congruence between flower morphology and bee behavior (*e.g.* if buzz-pollinated flowers and anther vibration by its visitors, and long corolla flowers visited through its entrance, not by lateral holes). Based on those observations we classified bees species as *pollinators* when, at least in half of their visits in a given plant species, they were observed visiting flowers as expected by flower morphology and contacting the anthers and stigma. On the other hand, a bee species was classified as *robbers* when it did not contact the flower's anthers and stigma and in all visits they did not behave as expected by flower morphology. For this paper we use "robber" as a generic term for all flower larcenists, thus including all kinds of robbers and thieves (for a review of the terminology of floral larceny see Irwin et al. 2010). The function of a bee (if either robber or pollinator) was recorded for each plant species, so a bee could be classified as pollinator for one plant species and as robber for another. Information about bee species, function and the plants they interact with are available as appendix (Supplementary material Appendix 1-2, chapter I).

Flower traits

In order to differentiate floral characteristics related to different trait matching models, we used the terms “complementarity traits” and “forbidden link traits” following the definitions of Santamaría and Rodriguez-Gironés (2007) and Vázquez et al. (2009a). All the traits described bellow were observed and measured in the field. Flower size measures for forbidden link models were taken from at least five fresh flowers from different plants using a caliper, and then we used the mean value of measurements. For plants with high size variable we measured up to 15 flowers.

The following floral traits were used to build the trait complementarity models: shape, color, symmetry and available resources. Flower types were classified into seven categories by their morphology and pollination mechanism following Faegri and Pijl (1979), Endress (1994), Westerkamp (1997) and Westerkamp and Claßen-Bockhoff (2007): dish (open flowers and those with corolla length shorter than 3mm), brush, keel, gullet-funnel (flowers with the corolla wide enough for a bee enter with at least their heads), tube (flowers with corolla tubes equal or longer than 3mm in which only mouthparts of visitors enters), bilabiate (flowers with dorsiventral organization and dorsal pollen transfer) and buzz (flowers with poricidal anthers pollinated by buzzing). Flower color was classified into six classes, based on the main visual spectra: blue; greenish-white (not pure white colors, with greenish, yellowish, or brownish white tonalities); pink; purple; red; white and yellow. Flower symmetry was classified in three classes (Neal et al., 1998): asymmetric, bilateral (monosymmetric, zygomorphy) and radial (actinomorphic, more than 2 plans of symmetry). Flower resource was determined either by direct observation of its presence as well by literature (Renner e Feil, 1993; Freitas e Sazima, 2003; Filho et al., 2011; Chauveau et al., 2012; Maia, 2013). As “resources available” we mean those that can be exploited by visitors without damaging flowers, during visits congruent to flower morphology. Those traits were used to build trait complementarity models.

The following measurements were used to build forbidden link models: main resource depth, width of flower opening and height of pollination chamber. Main resource depth was measured from the point where only mouthparts of flower visitors enters the flower to the nectar, it corresponds to the flower´s entrance in flowers with tube corollas or alignment channel for bilabiate and keel flowers (Westerkamp e Claßen-Bockhoff, 2007; Amaral-Neto et al., 2015).

Width of flower opening was measured as the transversal diameter at the corolla opening. Height of pollination chamber was taken as the height between the land platform of the flower, were pollinators rest when gathering flower resources, and the flower reproductive parts. For example, from bilabiate flowers it was taken from the lower lip to the upper lip (Westerkamp e Claßen-Bockhoff, 2007) and at malvaceous and convouvulaceous flowers, from the petals to anthers. We classified measured flower parts into 4 classes: short or small, ranging from 0.5 to 3 mm; medium, when ranging from 3 to 7 mm; long or large, when having more than 7 mm, and; non-restrictive when the variable appears not to exert any morphological constraints to bees, *e.g.* in open swallow nectar-flower (corolla length smaller than 0.5mm) or when anthers of pollen-flowers are exposed the main resource is depth was considered non-restrictive. The same is true in relation to flower opening when bees do not need to enter the flower or they only introduced their mouthparts. Some plants with highly variable values, whose measurements falls into two different size classes were included in both, for example, flowers with main resource depth ranging from 5 (medium class) to 10 (long class) were included into both medium and long main resource depth class. Finally, based on flower morphology and the resource available we determined whether specific behaviors are required from the main pollinator in order to obtain the flower resource. We noted four different behaviors of pollinators related to the following flower traits: (1) buzzing, required when the flowers have poricidal anthers in order to collect pollen; (2) oil collecting, when the main flower resource is oil; (3) strength, when the flower mechanism requires that the bees uses it strength to exploit flower resources, assigned only to keel flowers (Córdoba and Cocucci 2011; Amaral-Neto et al. minor review), and; (4) none, if flower resource was exploited without any specific behavior of visitors.

Bee traits and trait matching

Based on our field observations of the interactions we related the following traits from bees with the flower parts indicated in parenthesis: mouthpart length (main resource depth), measured from the labrum until the tip of the glossa; intertegular distance (width of flower opening), and; bee height (height of the pollination chamber), measured in the mesosoma. Measurements were taken using a caliper from all available died captured specimens for a given species, up to five individuals. When both male and female bees were available, three specimens from each sex were measured. We classified the structures into the same classes

and with the same ranges as those used for plant traits. Nonetheless, during our field observations we noted that some bees a little smaller or larger than flowers can effectively visit them. For example, bees with short mouthparts can reach nectar from flowers by inserting part of their heads within corolla tubes, or bees larger than flower opening can force their entrance. Bees within 0.5 mm deviation from classes limits (2.5–3.5 mm or larger than 6.5 mm) observed interacting with larger or smaller flowers, were included in both size classes to reflect these adjustments. For all bees we also assigned a fourth class of measurement called "non-restrictive" which coincide with the homonymous class of flowers. In this way, all bees, irrespectively of their measurements, were considered to fit a given flower when it exhibit a non-restrictive trait. Note that a flower can have a non-restrictive "main resource depth", which would fit all bee mouthparts, but simultaneously can have a "large height of pollination chamber" which fit only to large bees.

We also used direct observations and available literature (Silveira et al., 2002; Nunes-Silva et al., 2010) to assign specific behaviors to bees such as buzzing, oil collecting, strength or none, if the bee species don't show any of those behaviors.

Matrix construction

We excluded all observed robbery interactions and used the remaining ones to build a single quantitative **bee-plant network** (**BP**), which corresponds to the matrix we want to predict. In this matrix rows correspond to bees (*b*) and columns to plant species (*p*) and cell entries represents the number of recorded interactions between a pair of bee and plant species (BP_{bp}).

For temporal overlap matrix cell entries were expressed by the number of months in which a pair of plant and bee species co-occurred. This matrix was also normalized to produce the **phenological overlap** (**T**) probability matrix.

We used the observed interactions, including robbery, to build matrices where rows correspond to bee species and columns correspond to one of the categories of complementarity traits described in the previous section. In this way, we have four bee-flower trait matrices: bee-color, bee-flower type, bee-symmetry, bee-resources available. The cell values in those matrices were normalized dividing each cell by the matrix sum, in a manner that elements added up to one, resulting in a probability matrix. Then, we assigned the obtained probabilities to each bee-plant species interactions observed in the BP network based on the flower traits

exhibited by a given plant species. When more than one plant species had the same trait category, we divided the probability equally among all those plants. Thus, for example, all plants with yellow flowers have the same probability to be visited by a given bee species. Based on that, we obtained the trait complementarity probability matrices for: **flower color** (**C**), **flower type** (**F**), **symmetry** (**S**) and **resources available** (**R**). These probability matrices were then normalized to sum one.

For the forbidden links models we built four probability matrices: **corolla length** (**crl**), **flower opening** (**opn**), **flower height** (**hei**) and **behavior** (**beh**). Abbreviations with lowercase letters were used for morphological match matrices to more easily discriminate them from trait complementarity matrices. In those matrices interactions between a plant and given bee were allowed based on morphological match following different rules: (1) for **crl** matrix interactions were allowed when bee's mouthparts had equal or longer length category than the main resource depth; (2) for **hei** and **opn** matrices interactions were allowed only when bees had the same height and intertegular distance length class as height of pollination chamber and flower opening, respectively; (3) for **beh**, interactions were allowed when bees could exhibit the required behavior described in the previous section. Based on these rules, allowed interactions were assigned the value one, and those treated as forbidden received a zero. These matrices were also normalized in the same manner as done for the others.

We used the temporal overlap, the four forbidden links and four trait complementarity matrices to constructed probability matrices with combinations between two of them at a time, resulting in a total of 36 combined matrices. These matrices were obtained by elementwise product and were also normalized. Lastly, we formulated a null model (**NULL**), in which all pairwise interactions between bees and plants have the same probability. The non-combined matrices abbreviations and descriptions are showed at Table 1.

Network structure prediction

We evaluated if interaction probabilities derived from trait complementarity, forbidden links, and phenological overlap were able to predict the following properties from observed BP aggregated statistics (metrics): network specialization (H_2'), Connectance (*C*) and weighted nestedness (*WNODF*), and for bees and plants mean specialization (*d'*), mean degree (*k*) and mean number of shared partners (*shp*). We used a randomization algorithm by Vázquez et al.

(2009) implemented in the software R (R Development Core Team, 2014), modified in order to give the desired metrics. The randomization algorithm generated 100 random quantitative networks were the total number of interactions originally observed in the bee-plant matrix were assigned according to the probability matrices defined by our 46 models (the null model, four complementarity traits, four forbidden links traits and 36 combined matrices), with the only constraint that each species received at least one interaction. Aggregated statistics values for each random network were used to create an expected distribution for these metrics against which we compared the observed values for the BP network. The observed values that fall within the 95% confidence interval of the generated networks provide evidence that the biological mechanisms included in our models were enough to predict the structural properties within the range of those of observed network.

Besides structural network properties, we used those models to predict the observed pairwise interaction frequencies. The predictive ability of each model was estimated by the Akaike's information criterion (AIC) for each model (details in (Vázquez et al., 2009b). To compare the relative fit of competing models, we calculated ΔAIC values as the difference between the AIC generated by the observed function/plant and the observed network and each alternative model. We performed all calculations in R software ver. 3.1.0 (R Development Core Team, 2014) using the *bipartite* v 2.4 statistical packages (Dormann et al., 2008), and functions provided by Vázquez et al. (2009; Supplementary material).

Results

We documented 9,441 pollination visits distributed among 108 plant and 198 bee species. Asteraceae (43 species) and Fabaceae (ten species) were the most common plant families. Almost 50% of plant species had a long flowering phenology: 45 plant species flowered for more than six months and five species flowered for ten months (see Supplementary material Appendix 1). The most common plants complementarity traits were white color (30), tubular flower type (46), radial symmetry (80) and flowers where both pollen and nectar were available (60) (Supplementary material Appendix 1 of the first chapter). Concerning forbidden links, most plants did not exhibit restrictions for bee visitation for each measured trait. More than 90 plant species were classified as having non-restrictive flower opening width and pollination chamber height, and did not require any specific behavior from pollinators. The main resource depth had

more restrictive properties with only 41 plants included in non-restrictive category (Supplementary material Appendix 3).

For the 198 bee species, only 26 were recorded for more than 6 months, with four of them active all year long (Supplementary material Appendix 2). The majority of them belonged to the medium class of mouthpart length (136) and intertegular distance (115). Bee height was dominated by small bees (112) and most bees were able to perform some kind of specialized behavior, with a considerable number of them able to buzz (87) (Supplementary material Appendix 4).

The network was significantly less nested and connected than expected by null models (*WNODF*=13.45, null model confidence interval between 39.98 and 42.90; *C*=0.04, null models between 0.066 and 0.067), but more specialized (H_2'=0.50, null models ranging from 0.051 to 0.057). Plants were more specialized (d'=0.41), with less interaction partners (degree=4,63) and shared less mutualistic partners (number of shared partner=0.41) than bees (d'=0.39; degree = 8.5; number of shared partners=1.06).

In general, models combining two complementarity traits were the best predictors of network structure, excepted for bee and plant specialization where combinations of forbidden links and complementarity traits performed better (Figure 1). Almost all combinations of two trait complementarity models (excepting CT and ST) were able to predict three out of nine metrics (*WNODF*, shp_{bee} and shp_{plant}). None of the models were able to predict the other network properties, although very close values of connectance and both bee and plant degree were reached. Different combinations of complementarity traits had variable importance regarding the analyzed propriety, however models including flower type and color were always among the two best predictors.

For bee specialization (d'_{bee}) models including required behavior were the best, while for d'_{plant} models with corolla length improved prediction. Usually models with one or with combinations between forbidden links performed poorly.

The color-temporal (CT) model provided the best fit to the observed species pairwise interaction frequencies in the likelihood analysis, although it had an extremely large ΔAIC of 31941.27. The second best model was the flower type-temporal (FT), with a large difference (1168.97) from the CT model (see Fig 2 for full likelihood results). The worst models (with higher

ΔAIC values) were NULL, and models with only one forbidden link. However the best models pointed out by AIC had poor explanative power when compared to the BP (observed) matrix when fitted to itself, indicating that much remains unexplained.

Discussion

Why forbidden link models were poor predictors of bee-plant networks?

Trait matching is not usually pointed out as the main determinant of network structure, but there is an agreement that forbidden links increase prediction power of models for plant-animal interactions (Krishna et al., 2008; Vázquez et al., 2009b; Olito e Fox, 2014). Against this growing consensus, floral restrictions to the access of floral resources, both forbidden links and phenological uncoupling, were the most important determinants of network properties in some recent studies (Junker et al., 2013; Vizentin-Bugoni et al., 2014). The present work, however, points towards a modest importance of forbidden links for bee-plant interaction networks.

The reduced importance of forbidden links and phenological overlap found in our study is due to the fact that the majority of plants had low complexity flowers with long flowering phonologies, which imposes weak constraints to bee-plant interactions. Thus, on forbidden links and phenological overlap models most of interactions are able and had the same probability to occur, due to the lack of constraints, and just few interactions are in fact restricted. This is a similar explanation as observed for a plant-pollinator network at Seychelles which was also dominated by non-morphological restrictive flowers, and where the authors also found weak explanatory power of models based on traits (Kaiser-Bunbury et al., 2014).

Corolla depth is usually the only trait used as limiting morphological matching between plant and flower visitors (Vázquez et al., 2009b; Olito e Fox, 2014; Vizentin-Bugoni et al., 2014). Although resource depth is the main constraint in many pollinators (Faegri e Pijl, 1979; Endress, 1996), bee-pollinated flowers exhibit a wide range of other morphological restrictions which reflects not only the morphological but also behavioral diversity in this group of pollinators (Faegri e Pijl, 1979; Buchmann, 1983; Endress, 1996; Westerkamp, 1997). Besides corolla depth, behavioral aspects of pollinators were found to strongly influence specialization (*d'*) of plants and bees. The fact of flower type-behavior and flower type-corolla length were the best predictors of specialization for bees and plants, respectively, reflects the importance of those traits in delimiting pollination niche. Nonetheless these restrictive features with strong influence

in pairwise bee-plant interactions are diluted when they are viewed against a matrix dominated by flowers showing no restrictions, which frequently is the prevalent scenario (Machado e Lopes, 2004; Freitas e Sazima, 2006). Thus, in more morphologically restrictive networks flower traits have a stronger influence shaping network structure, as proposed by Kaiser-Bunbury et al. (2014) and actually observed in a network of interactions between hummingbirds and flowers were corolla and bill lengths were the morphological constraints to interactions (Vizentin-Bugoni et al., 2014).

Our study also contrasted with previous findings where the temporal aspect alone had a stronger effect on network properties (Olesen et al., 2008; Junker et al., 2013). Most of our plant species have long flowering times and therefore do not impose strong phenological constraints to interactions with bees with different flight periods. For example, *Baccharis uncinella* and *Chrysolaena lithospermifolia* had flowering times that ranges for ten months (absent only in the coldest months of July and August, where pollinator activity is also low) and they had the same probability to interact with *Melissoptila similis* and *Ptilothrix fructifera* which were observed only respectively on January and February, and November and December, if temporal overlap is the only constraint. That means pollinators in activity in different periods of the year could rely on the resources provided by the same long flowering plants. Thus, phenological constraints are restricted to few pairwise interactions while most of restrictions were due to constraints other than phenological uncoupling.

Phenological uncoupling is more important in habitats where organisms intrinsically have short phenophases and its influence is almost none in communities with perennial interacting species (Olesen et al., 2011). Previous studies found that interactions are highly influenced by phenological overlap between plant and animals (Olesen et al., 2008; Vizentin-Bugoni et al., 2014). Opposing our findings, species on these studies had short phenophases and a large proportion of interactions were forbidden due to the temporal uncoupling, even between species without morphological restrictions (Olesen et al., 2008; Vizentin-Bugoni et al., 2014). On the other hand, when both plant and animals had long coupled phenophases, the probability of they to interact is high (Olesen et al., 2008, 2011), which results in the minor explanatory significance of spatial and temporal variation on plant–pollinator interactions (Kaiser-Bunbury et al., 2014). Together with previous findings it seems that when species have

very restricted phenophases temporal uncopling have higher influence shaping the structure of networks (Olesen et al., 2008; Vizentin-Bugoni et al., 2014), otherwise, when flowering and activity period of pollinators extended for long time, other factors have a more important role as in the present study and others (Olesen et al., 2011; Kaiser-Bunbury et al., 2014). This tendency should be focused in further studies.

All single trait models have much better prediction power when coupled with temporal model (Figures 1 and 2), indicating that although temporal overlap is not the main determinant of interactions, network structure is strongly influenced by this aspect. A striking example is the interactions of *Jacaranda oxyphylla* which was observed flowering for ten different months although only interacted with eight pollinator species. This bilabiate flower type species has morphological constraints and it is pollinated by large-bodied bees. Otherwise, *Chrysolaena lithospermifolia* that bloomed during the same 10 months, had its non-restrictive flowers pollinated by 37 bee species. This example illustrates how temporal overlap coupled with other traits generates specific probabilities for pairwise interactions, which increase the prediction power of network properties of models.

Why complementarity trait models were good predictors of bee-plant networks?

Animal choices toward flowers involve not only morphological matching but they also relate to preference to or aversion against specific flower traits such as symmetry, color, presence of nectar and energy uptake (Lehrer et al., 1995; Lunau et al., 1996, 2011; Cakmak et al., 2009). Some studies showed that flower colors and scent coupled with other factors may influence network topology acting as filters, promoting or inhibiting some interactions (Junker et al., 2010; Renoult et al., 2014). We found that models coupling different complementarity traits or the association between a forbidden link and a complementarity trait are good predictors of network aggregated statistics, despite their poor performance when analyzed in isolation. This is in accordance to Santamaría and Rodriguez-Gironés (2007) who found an improvement to the prediction of network structures in models with multiple mechanisms. Our trait complementarity models performed better than forbidden links simply because they generate more distinct probabilities for pairwise interactions to occur. In the first chapter we discussed the importance of probability distribution among observed interactions on model ability to predict aggregated statistics. We discussed that when some groups of interacting species have similar

probabilities to interact, the same network structure can be achieved by randomly distributed interactions in any pair of species (in that case, pair of bee function and plant species). In the other extreme, when there is no constraints to species interactions and many species have the same interaction probabilities, as experienced at our forbidden link models, it results in very connected networks (all interactions are possible and equally probable to occur), similar to those generated by NULL models (see Figure 1 - Connectance). Thus, our models which combined any two mechanisms, forbidden links traits, complementarity traits or temporal overlap, had better predictive function than single trait models and combinations between trait complementarity models and temporal overlap are the best ones due to assigned more distinctive probabilities to pairs of interactive species. The poor prediction of single complementarity models opposing to the results of the first chapter is due to the high number of bees (198) compared to the low number of functions (2), thus a single complementarity trait also results in similar probabilities to large number of plant-bee pairs.

Do forbidden links and trait complementarity predict pairwise interactions?

Usually the best models to predict network properties were not the best to predict pairwise species interactions (Vázquez et al. 2009b; Vizentin-Bugoni et al. 2014; Olito and Fox 2014; Amaral-Neto et al. First chapter). However our model with lower ΔAIC (color-temporal model) generated distributions closer to observed connectance, nestedness, and bee and plant degree. The second best model (flower type-temporal) was also the best to predict connectance and species degree. This indicates that those traits are assigning probabilities to pairwise interactions in the models in a similar way to those observed in the bee-plant network. The same pattern as in model prediction is observed in pairwise prediction were temporal overlap alone is one of the worst predictors, although highly improving models when coupled with other traits. Color innate and learned preferences of bees are long known to drive choices during foraging for resources (Lunau e Maier, 1995; Lunau et al., 1996) but only more recently studies showed its relative importance in a network context (Junker et al., 2013; Renoult et al., 2014). Color consists in a multidimensional signal and because of this it is hard to measure (Lunau e Maier, 1995; Renoult et al., 2014). Despite of that, simple utilization of the main visual spectra of this parameter as a mechanism of trait complementarity, seems to give good answers on its effects on network structure. However, a more detailed definition of the color components of

flowers and incorporation of information on sensorial apparatuses and bee innate preferences should further improve the understanding about the responses due to colors in the network structure.

Prediction of network aggregated statistics by trait matching mechanisms

Our study leads the discussion about the determinants of network structure a step further by detailing the influence of trait matching mechanisms. We showed that consideration of multiple aspects of trait complementarity and forbidden links may lead to more precise models which are able to simulate network structure. In this sense trait matching could appear more commonly as a better predictor of aggregated statistics instead of the current vision of its function as an improvement for other models such as those incorporating spatiotemporal features and abundance (Krishna et al., 2008; Vázquez et al., 2009b; Olito e Fox, 2014). Nonetheless further studies should improve the classification methods for complementarity traits, in particular those related to flower color, in order to take in consideration more detailed data on the pollinators' sensorial apparatuses. Due to differences in the sensorial apparatus, morphology and behavior of flower visitors, we also expect that different mechanisms are more or less important regarding the functional group of pollinators involved. For example, corolla length and scentless vivid colored flowers may play an important role in hummingbird pollinated plants (Faegri e Pijl, 1979; Vizentin-Bugoni et al., 2014) but it has less influence in beetle and nocturnal moth pollinated plants where scents and floral temperature are important factors (Faegri e Pijl, 1979; Varassin e Amaral-Neto, 2015).

Using multiple trait matching mechanisms may lead to a better comprehension about which traits matter most in determining which pollinators visit which flowers, as suggested by Ollerton et al. (2009). This approach may also be useful in finding the suits of phenotypic floral traits correlated with particular effective functional groups of pollinators (Faegri e Pijl, 1979; Endress, 1996; Fenster et al., 2004). In this sense it would improve identification of functional flower traits and functional groups in pollination networks with many distinct groups of pollinators.

Besides that, this approach appears to lead to models that could predict both network aggregated statistics and pairwise interactions since the probabilities are assigned to interactions which fit in many specific traits. Considering that modules reflect pollination

syndromes and groups where trait evolution is strongly affected by interactions within them (Olesen et al., 2007; Danieli-Silva et al., 2012), and that compartmentalization is a pervasive feature of mutualistic networks (Olesen et al., 2007; Vázquez et al., 2009a), we propose that further studies should use multiple trait matching models to predict both modularity and module composition of networks.

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TABLES

Table 1. Models descriptions.

Model/Matrix abbreviation	Description
BP	Observed interactions between bees and plants species
T	Temporal overlap
C	Visits are determined solely by flower color
F	Visits are determined solely by flower type
R	Visits are determined solely by resources available
S	Visits are determined solely by flower symmetry
crl	Visits are determined by match between bee's mouthparts and main resource depth
opn	Visits are determined by match between bee's intertegular distance and width of flower opening
hei	Visits are determined by match between bee and flower's height
beh	Visits are allowed for bees which exhibit a given behavior required to flower mechanism activation or resource collecting
NULL	All interactions have the same probability

Notes: Combined probability models are calculated as the element-wise product between single trait probability models. They were abbreviated by coupling the correspondent single trait probability models abbreviations, using underline "_" when one of the models corresponds to a forbidden link trait. (*e.g.*: CS = color-symmetry model, C_beh = Color-behavior model).

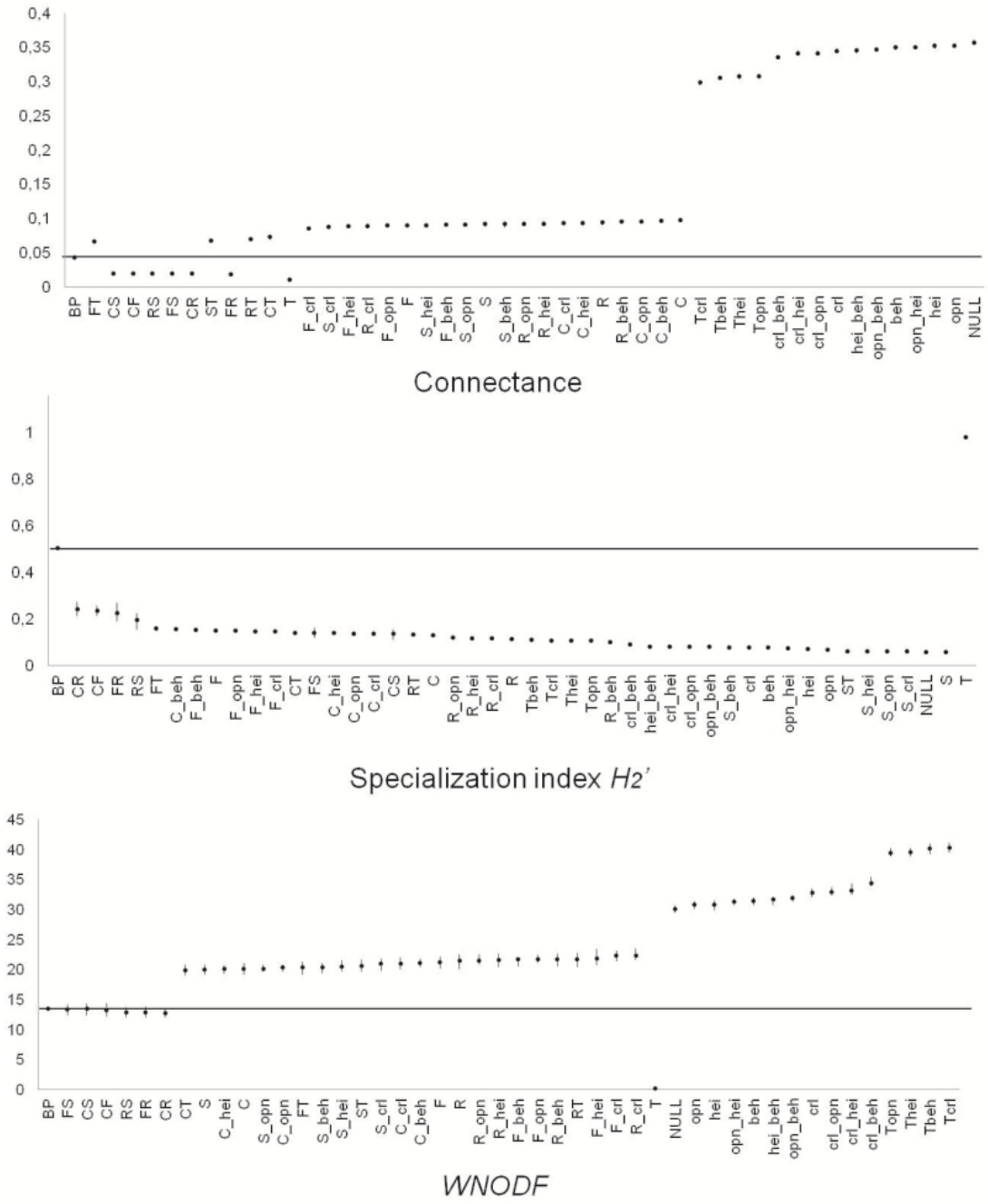

Figure 1. Values of aggregate network statistics (circles, mean; bar, 95% confidence interval) produced by 100* randomizations of all probabilistic matrices in relation to the observed value (horizontal line). The probabilistic matrices are based on phenology (**T**), trait complementarity – flower type (**F**), available resource (**R**), color (**C**) and symmetry (**S**) - and, forbidden links – corolla length (**crl**), pollination chamber heigh (**hei**), opening width (**opn**) and behavior (**beh**), and combinations of them. **NULL** is a null model in which all interactions had the same probability. (Continue on next page).

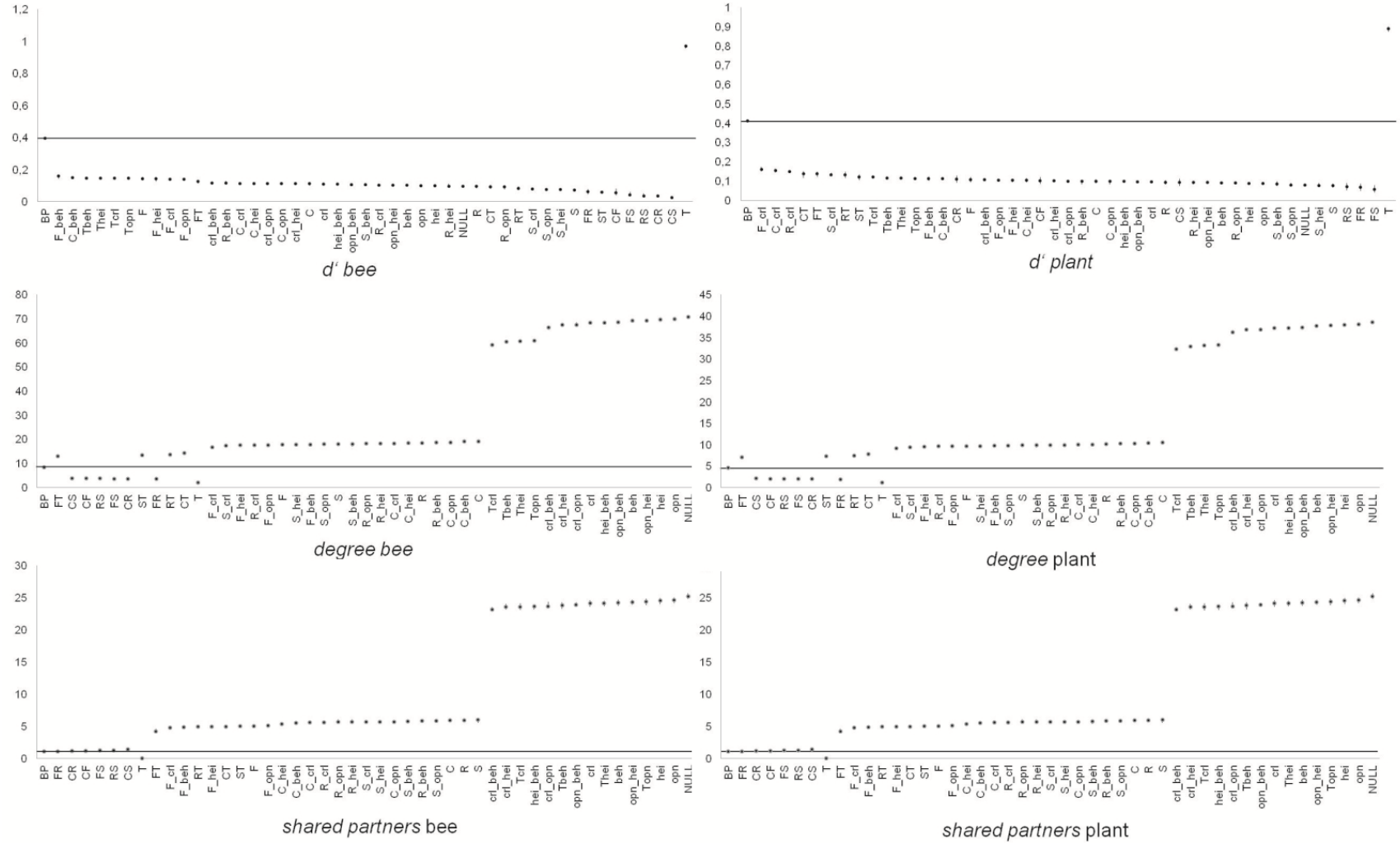

Figure 1. Cont. Values of aggregate network statistics (circles, mean; bar, 95% confidence interval) produced by 100* randomizations of all probabilistic matrices in relation to the observed value (horizontal line).

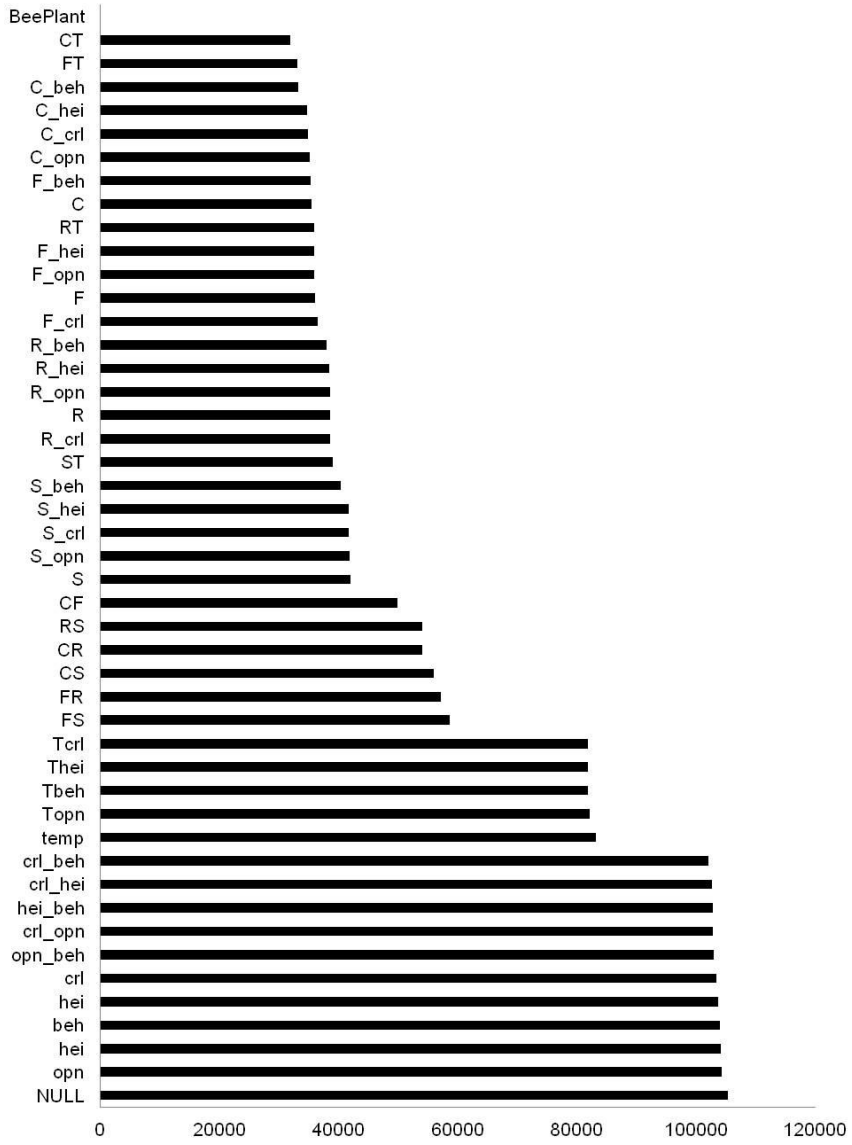

Figure 2. Comparison of ΔAIC values of the probabilistics matrices with the value obtained by fitting the observed bee-plant network to itself. Models were based on phenology (**T**), trait complementarity – flower type (**F**), available resource (**R**), color (**C**) and symmetry (**S**) - and, forbidden links – corolla length (**crl**), pollination chamber heigh (**hei**), opening width (**opn**) and behavior (**beh**), and combinations of them. **NULL** is a null model in which all interactions had the same probability. Shorter bars represent better models.

Supplementary material

Appendix 1. Plant phenology

Family and Plant species	Jan	Fev	Mar	Abr	Mai	Jun	Jul	Ago	Set	Out	Nov	Dez	Cumulative number of months
Amaranthaceae													
Pfaffia tuberosa (Spreng.) Hicken	1	0	1	1	1	0	0	0	0	1	1	1	7
Apiaceae													
Eryngium elegans Cham.&Schlecht.	1	1	0	0	0	0	0	0	1	1	1	0	5
Eryngium junceum Cham.	1	1	1	0	0	0	0	0	1	0	0	1	5
Arecaceae													
Allagoptera campestris (Mart.) Kuntze	1	1	1	1	1	0	0	0	1	1	1	1	9
Butia microspadix Burret.	1	0	0	1	0	0	0	1	1	1	1	0	6
Asteraceae													
Aspilia foliacea (Spreng.) Baker	1	0	1	1	0	0	0	0	1	1	1	1	7
Aspilia montevidensis (Spreng.) Kuntze	1	0	1	1	1	1	0	1	1	1	1	1	10
Asteraceae sp.4	1	0	1	1	0	0	0	0	1	1	1	1	7
Baccharis articulata (Lam.) Persoon	1	0	1	0	0	0	0	0	1	1	1	1	6
Baccharis crispa Spreng.	1	0	1	0	0	0	0	1	1	1	1	1	7
Baccharis dracucunlifolia DC.	1	0	1	1	0	0	0	0	1	1	1	1	7
Baccharis linearifolia (Lam.) Pers.	0	1	1	1	0	0	0	0	0	0	1	1	5
Baccharis myricaefolia DC.	1	0	0	1	0	0	0	0	0	0	0	1	3
Baccharis trilobata A.S.Oliveira & Marchiori	1	1	1	1	1	1	0	0	1	0	0	0	7
Baccharis uncinella DC.	1	1	1	1	1	1	0	0	1	1	1	1	10
Baccharis verticilata	1	0	1	0	0	0	1	1	1	0	0	0	5
Calea cuneifolia DC.	1	1	1	1	0	0	0	0	0	0	1	1	6

Calea hispida (DC.) Bak.	1	1	1	1	0	0	1	1	1	1	1	1	10
Calea longifolia Gardner	1	1	1	1	1	0	0	0	1	0	1	1	8
Calea monocephala Dusén	1	1	1	0	0	0	0	0	1	0	0	1	5
Calea platylepis Sch.Bip. ex Baker	0	0	1	0	0	0	0	0	1	0	0	1	3
Chromolaena congesta (Hook. & Arn.) R.M.King & H.Rob.	0	0	1	1	0	0	0	1	1	1	0	0	5
Chromolaena laevigata (Lam.) R.M.King & H.Rob.	1	1	1	1	0	0	0	0	1	1	1	0	7
Chrysolaena lithospermifolia (Lam.) R.M.King & H.Rob.	1	1	1	1	1	1	0	0	1	1	1	1	10
Disynaphia caliculata (Hook. & Arn.) R.M.King & H.Rob.	1	1	1	1	0	0	0	0	0	0	1	1	6
Elephantopus mollis Kunth	1	0	0	0	0	0	0	0	0	0	1	1	3
Eupatorium aff. *laevigatum*	1	1	1	1	1	0	0	0	1	1	1	1	9
Eupatorium multifidum DC.	1	1	1	1	1	0	0	0	1	1	1	1	9
Gochnatia polymorpha (Less.) Cabrera	0	0	1	0	0	0	0	0	1	0	1	0	3
Grazielia intermedia (DC.) R.M.King & H.Rob.	1	1	1	1	0	0	0	0	1	1	1	1	8
Heterocondylus reitzii R.M.King & H.Rob.	1	0	1	1	0	0	0	1	1	0	0	0	5
Hypochaeris radicata L.	1	0	0	0	0	0	0	0	0	0	1	1	3
Isostigma speciosum Less.	1	1	1	0	1	0	0	0	1	1	1	1	8
Lessingianthus argenteus (Less.) H.Rob.	1	1	1	1	0	0	0	0	0	1	0	1	6
Lessingianthus grandiflorus Less.	1	1	1	1	1	1	0	0	0	1	1	1	9
Lessingianthus polyphyllus (Sch.Bip. ex Baker) H.Rob.	1	1	1	1	1	0	0	0	0	0	0	0	5
Lessingianthus simplex (Less.) H.Rob.	1	0	0	0	0	0	0	0	0	1	0	1	3
Mikania hirsutissima DC.	1	0	0	0	0	0	0	1	0	0	0	0	2
Piptocarpha axillaris (Less.) Baker	1	1	1	0	0	0	0	1	1	0	0	1	6
Pterocaulon angustifolium DC.	1	1	1	1	0	0	0	0	1	1	0	0	6
Senecio brasiliensis (Spreng.) Less.	1	1	1	1	1	0	0	0	1	1	1	1	9
Senecio oleosus Vell.	0	0	0	0	1	1	0	1	1	1	1	1	7
Solidago chilensis Meyen	1	0	0	1	0	0	0	1	1	0	0	1	5
Stenocephalum megapotamicum (Spreng.) Sch.Bip.	1	0	1	1	1	0	1	1	0	1	0	1	8
Trichocline speciosa Less.	0	0	0	1	1	1	1	1	0	0	0	0	5

Verbesina sordences DC.	1	1	1	1	0	0	0	0	0	0	1	1	6
Vernonanthura nudiflora (Less.) H.Rob.	1	1	1	1	0	0	0	0	1	1	1	1	8
Vernonanthura oligolepis (Sch.Bip.) H. Rob.	1	1	1	1	0	0	0	0	1	0	1	0	6
Vittetia orbiculata (DC.) R.M.King & H. Rob	0	0	1	1	1	0	0	0	0	0	0	0	3
Bignoniaceae													
Jacaranda oxyphylla Cham.	1	0	1	1	1	1	0	1	1	1	1	1	10
Boraginaceae													
Moritzia dusenii I.M.Johnst.	1	0	1	1	0	0	0	0	1	1	1	1	7
Clethraceae													
Clethra scabra Pers.	1	0	0	0	0	0	0	0	0	0	0	1	2
Convolvulaceae													
Ipomoea maurandioides Meisn.	1	0	1	1	1	0	0	0	0	1	1	1	7
Ericaceae													
Agarista pulchella * Cham. ex G.Don	1	1	1	1	0	0	0	1	1	1	1	1	9
Euphorbiaceae													
Croton antisyphiliticus Mart.	0	0	1	1	1	1	0	1	1	1	0	1	8
Croton heterodoxus Baill.	1	0	0	1	0	0	1	1	1	1	0	1	7
Fabaceae													
Chamaecrista desvauxii (Collad.) Killip	1	1	1	0	0	0	0	0	0	0	0	1	4
Chamaecrista punctata (Vogel) H.S.Irwin & Barneby	1	1	1	0	0	0	0	0	1	1	1	1	7
Collaea speciosa (Loisel.) DC.	1	1	1	1	1	0	0	0	1	1	1	0	8
Crotalaria micans Link	1	0	1	0	0	0	0	0	1	0	0	1	4
Eriosema glabrum Mart. ex Benth.	1	0	0	0	0	0	0	1	1	0	1	1	5
Eriosema heterophylum Benth.	0	0	0	0	0	0	0	0	0	0	1	0	1
Galactia neesii DC.	1	0	1	0	0	0	0	0	1	1	1	1	6
Macroptilium prostratum (Benth.) Urb.	1	0	1	1	0	0	0	0	0	0	1	1	5
Pomaria stipularis (Vogel) B.B.Simpson & G.P.Lewis	1	1	1	1	0	0	0	0	0	0	0	0	4

Gesneriaceae													
Sinningia allagophylla (Mart.) Wiehler	0	0	0	0	0	0	0	0	0	1	1	0	2
Iridaceae													
Gelasine coerulea * (Vell.) Ravenna	0	0	0	0	0	0	0	0	1	0	1	1	3
Sisyrhinchium micranthum Cav.	0	0	0	1	0	0	0	1	0	0	0	1	3
Sisyrinchium brasiliense (Ravenna) Ravenna	1	1	1	1	0	0	0	0	1	0	0	1	6
Sisyrinchium restioides Spreng.	0	0	0	0	0	0	0	1	1	0	0	0	2
Sisyrinchium vaginatum Spreng	1	0	1	1	0	0	0	1	1	0	1	1	7
Lamiaceae													
Peltodon rugosus Tolm.	0	0	1	1	0	0	0	1	1	1	1	1	7
Rhabdocaulon gracile (Benth.) Epling	0	0	1	1	1	0	1	1	0	0	0	0	5
Rhabdocaulon lavanduloides (Benth.) Epling	1	0	0	1	1	0	0	0	1	0	1	1	6
Salvia aliciae E.P.Santos	0	1	1	0	0	0	0	0	1	1	1	1	6
Salvia lachnostachys Benth.	1	1	1	1	1	0	0	0	1	1	1	1	9
Hyptis apertiflora Epling	0	0	0	0	0	0	0	0	1	1	1	1	4
Lobeliaceae													
Lobelia camporum Pohl	1	0	1	1	0	0	0	0	1	0	0	0	4
Lythraceae													
Cuphea glutinosa Cham. & Schltdl.	1	0	1	0	0	0	0	0	0	0	1	0	3
Cuphea linarioides Cham. & Schltdl.	1	0	1	1	1	0	0	0	0	1	1	1	7
Malpighiaceae													
Aspicarpa pulchella (Griseb. ex Mart.) O'Donell & Lourteig	1	0	1	1	0	1	0	0	0	0	1	1	6
Byrsonima intermedia A. Juss.	1	0	0	0	0	0	0	0	1	1	1	1	5
Byrsonima psilandra Griseb.	0	0	1	0	0	0	0	0	0	0	1	1	3
Malvaceae													
Hibiscus sp. *	0	0	1	1	1	0	0	0	1	1	1	0	6
Peltaea edouardii (Hochr.) Krapov. & Cristóbal	0	1	1	1	0	0	0	0	1	0	1	1	6
Sida macrodon DC.	1	0	1	1	0	0	0	0	0	1	1	0	5

Sida sp.	1	1	1	0	0	0	0	0	1	1	1	1	7
Melastomataceae													
Acisanthera alsinaefolia (Mart. & Schrank ex DC.) Triana	1	1	1	1	0	0	0	0	0	0	0	1	5
Leandra simplicicaulis (Naudin) Cogn.	0	1	1	1	1	0	0	0	1	0	1	0	6
Miconia theizans (Bonpl.) Cogn.	1	0	1	0	0	0	0	0	0	0	1	0	3
Miconia hyemalis[*] A.St.-Hil. & Naudin	1	1	1	1	1	0	0	0	1	0	0	0	6
Tibouchina gracilis (Bonpl.) Cogn	1	0	1	1	0	0	0	1	1	1	1	1	8
Tibouchina martialis Cogn.	0	0	0	0	0	1	0	0	1	1	0	1	4
Mimosaceae													
Mimosa dolens var. *acerba* (Benth.) Barneby	1	1	1	1	1	0	0	0	1	1	1	1	9
Mimosa dolens var. *rudis* (Benth.) Barneby	1	1	1	1	1	0	0	0	0	0	0	0	5
Myrtaceae													
Campomanesia adamantina [*] (Cambess.) O.Berg.	0	0	0	0	0	0	0	0	1	1	0	0	2
Myrtaceae sp2	0	0	0	0	0	0	0	0	0	0	1	1	2
Myrtaceae sp3[*]	0	0	0	0	0	0	0	0	1	0	1	1	3
Passifloraceae													
Piriqueta taubatensis (Urb.) Arbo	0	0	1	0	0	0	0	0	0	0	0	0	1
Plantaginaceae													
Angelonia integerrima Spreng,	1	1	1	1	1	0	0	0	1	1	1	1	9
Rhamnaceae													
Rhamnus sphaerosperma Sw.	1	0	1	1	1	0	0	0	1	1	1	1	8
Rubiacae													
Borreria poaya (A.St.-Hil.) DC.	1	0	1	1	1	0	0	0	0	1	1	1	7
Borreria verticillata (L.) G. Mey	1	0	0	0	0	0	0	0	1	0	1	1	4
Borreria paranaensis E.L.Cabral & Bacigalupo	1	0	0	1	0	0	0	0	0	0	1	1	4
Galianthe elegans E.L.Cabral	1	0	1	1	1	0	0	0	1	1	1	1	8
Scrophulariaceae													
Buddleja elegans Cham. & Schltdl.	1	0	0	0	1	0	0	0	1	1	1	1	6

Solanaceae													
Calibrachoa linoides (Sendtn.) Wijsman	1	1	1	0	0	0	0	0	1	1	1	1	7
Solanum aculeatissimum Jacq.	1	0	1	0	1	1	0	0	1	0	1	0	6
Solanum pseudocapsicum L.	0	0	0	0	0	1	1	0	1	1	1	0	5
Solanum reitzii L.B.Sm. & Downs	0	0	1	0	0	0	0	0	0	0	1	1	3
Verbenaceae													
Lippia hirta (Cham.) Schauer	1	0	1	1	1	0	0	0	0	0	0	0	4
Lippia lupulina Cham.	1	0	1	1	0	0	0	0	0	0	1	1	5
Verbena hirta Spreng.	1	0	1	1	1	0	0	0	1	1	1	1	8

Appendix 2. Bee phenology

Bee species	Jan	Fev	Mar	Abr	Mai	Jun	Jul	Ago	Set	Out	Nov	Dez	Cumulative number of months
ANDRENINAE													
Calliopsini													
Callonychium petuniae Cure & Wittmann, 1990	0	0	0	0	0	0	0	0	1	1	1	1	4
Oxaeini													
Oxaea flavescens Klug, 1807	0	0	1	0	0	0	0	0	0	0	0	0	1
Protandrenini													
Anthrenoides sp.	0	1	0	0	0	0	0	0	1	1	1	1	5
Psaenythia annulata Gerstaecker, 1868	1	1	1	1	1	0	0	0	1	1	1	1	9
Psaenythia bergii Holmberg, 1884	1	0	1	0	0	0	0	0	0	1	0	1	4
Psaenythia collaris Schrottky, 1906	0	0	0	0	0	0	0	0	0	0	1	0	1
Psaenythia quadrifasciata Friese, 1908	1	1	1	1	0	0	0	0	0	0	0	0	4
Psaenythia sp.2	0	0	0	0	0	0	0	0	0	1	1	0	2

Psaenythia sp.3	0	0	1	0	0	0	0	0	0	0	0	0	1
Rhophitulus reticulatus (Schlindwein & Moure, 1998)	0	0	0	0	0	0	0	0	1	0	1	0	2
Rhophitulus sp.1	1	1	0	0	0	0	0	0	0	0	0	0	2
APINAE													
Anthophorini													
Anthophora (Mystacanthophora) paranensis Holmberg, 1903	0	0	1	1	0	0	0	0	1	1	1	0	5
Apini													
Apis mellifera Linnaeus, 1758	1	1	1	1	1	1	1	1	1	1	1	1	12
Bombini													
Bombus (Fervidobombus) pauloensis Friese, 1913	1	1	1	1	1	0	0	0	1	1	1	1	9
Bombus brasiliensis Lepeletier, 1836	1	0	0	0	0	0	0	0	0	0	0	0	1
Bombus morio (Swederus, 1787)	1	1	1	1	1	0	0	0	1	1	1	1	9
Centridini													
Centris (Centris) nitens Lepeletier, 1841	0	0	0	1	0	0	0	0	0	1	0	0	2
Centris (Centris) varia (Erichson, 1849)	1	1	0	0	0	0	0	0	0	1	1	1	5
Centris (Hemisiela) tarsata Smith, 1874	0	0	1	0	0	0	0	0	0	1	1	1	4
Centris (Melacentris) sp.2 (aff. *C.discolor*)	0	0	0	0	0	0	0	0	0	0	1	0	1
Centris (Paracentris) burgdorfi Friese, 1900	1	0	0	0	0	0	0	0	0	1	0	1	3
Centris (Trachina) proxima Friese, 1899	0	0	0	0	0	0	0	0	0	1	1	1	3
Centris (Xanthemisia) bicolor Lepeletier, 1841	0	0	0	0	0	0	0	0	0	1	1	0	2
Epicharis (Epicharis) bicolor Smith, 1854	0	0	0	0	0	0	0	0	0	1	0	0	1
Epicharis (Epicharitides) iheringi Friese, 1899	1	0	0	0	0	0	0	0	0	0	1	1	3
Epicharis (Triepicharis) analis Lepeletier, 1841	0	0	1	0	0	0	0	0	0	0	0	0	1
Emphorini													
Ancyloscelis romeroi (Holmberg, 1903)	0	0	1	0	0	0	0	0	0	1	0	0	2
Melitoma segmentaria (Fabricius, 1804)	1	0	1	0	0	0	0	0	0	0	1	1	4
Ptilothrix cfr. *plumata*	0	0	1	1	0	0	0	0	0	1	1	1	5
Ptilothrix fructifera (Holmberg, 1903)	0	0	0	0	0	0	0	0	0	0	1	1	2

Ptilothrix plumata Smith, 1853	0	0	0	0	0	0	0	0	0	0	1	0	1
Ericrocidini													
Mesonychium coerulescens Lepeletier & Serville, 1825	0	0	0	0	0	0	0	0	0	0	0	1	1
Mesoplia rufipes (Perty, 1833)	0	0	0	0	0	0	0	0	0	0	0	1	1
Eucerini													
Dasyhalonia sp.	0	1	0	0	0	0	0	0	0	0	0	0	1
Gaesischia (Gaesischia) aff. *fulgurans*	0	0	1	1	0	0	0	0	0	0	0	0	2
Gaesischia (Gaesischia) fulgurans (Holmberg, 1903)	1	1	1	1	0	0	0	0	0	0	0	0	4
Gaesischia (Gaesischia) nigra Moure, 1968	0	0	0	1	0	0	0	0	0	0	0	0	1
Gaesischia (Gaesischia) undulata Urban, 1989	1	0	0	0	0	0	0	0	0	0	0	0	1
Gaesischia (Gaesischiopsis) aurea Urban, 1968	0	0	1	0	0	0	0	0	0	0	0	0	1
Gaesischia (Gaesischia) aff. *undulata*	0	0	1	0	0	0	0	0	0	0	0	0	1
Melissodes (Ecplectica) sexcincta (Lepeletier, 1841)	0	0	1	0	0	0	0	0	0	1	0	0	2
Melissoptila aureocinta Urban, 1968	1	0	0	0	0	0	0	0	0	0	0	0	1
Melissoptila larocai Urban, 1998	0	0	0	0	0	0	0	0	0	1	1	1	3
Melissoptila minarum (Bertoni & Schrottky, 1910)	1	0	1	1	0	0	0	0	0	0	0	0	3
Melissoptila paranaensis Urban, 1998	1	0	0	0	0	0	0	0	0	0	1	1	3
Melissoptila richardiae Bertoni & Schrottky, 1910	0	0	1	1	0	0	0	0	0	0	0	0	2
Melissoptila similis Urban, 1988	1	1	0	0	0	0	0	0	0	0	0	0	2
Thygater (Nectarodiaeta) mourei Urban, 1961	0	0	0	0	0	0	0	0	1	0	0	0	1
Thygater (Thygater) analis (Lepeletier, 1841)	0	0	1	0	0	0	0	0	0	0	1	0	2
Euglossini													
Eufriesea sp.1	0	0	0	0	0	0	0	0	0	0	1	1	2
Eufriesea sp.2	0	0	0	0	0	0	0	0	0	1	0	0	1
Exomalopsini													
Exomalopsis (Exomalopsis) analis Spinola, 1850	0	1	1	0	0	0	0	0	1	0	0	1	4
Exomalopsis (Phanomalopsis) sp.1	0	0	0	0	0	0	0	0	0	0	1	0	1

Exomalopsis dubia Silveira & Almeida, 2009	0	0	1	0	0	0	0	0	0	0	0	0	1
Isepeolini													
Isepeolus viperinus (Holmberg, 1886)	0	0	0	0	0	0	0	0	1	1	1	0	3
Meliponini													
Scaptotrigona bipunctata (Lepeletier, 1836)	0	0	1	0	0	0	0	0	0	0	0	0	1
Schwarziana mourei Melo, 2003	0	0	0	0	1	1	0	1	1	1	1	1	7
Trigona spinipes (Fabricius, 1793)	1	1	1	1	1	1	1	1	1	1	1	1	12
Nomadini													
Doeringiella (Orfilana) cingillata Moure, 1954	0	0	0	0	0	0	0	0	0	0	1	0	1
Thalestria spinosa (Fabricius, 1804)	1	0	0	0	0	0	0	0	0	0	0	0	1
Osirini													
Osiris sp.1	0	0	0	0	0	0	0	0	0	0	1	1	2
Parepeolus niger Roig-Alsina, 1989	1	0	1	0	0	0	0	0	0	0	0	1	3
Tapinitaspidini													
Tapinotaspoides serraticornis (Friese, 1899)	1	0	1	1	0	0	0	0	0	0	1	1	5
Caenonomada labrata Zanella, 2002	0	0	0	0	0	0	0	0	0	0	0	1	1
Arhysoceble dichroopoda Moure, 1948	0	0	0	0	0	0	0	0	0	1	1	0	2
Arhysoceble picta (Friese, 1899)	0	0	0	0	0	0	0	0	0	1	0	0	1
Arhysoceble sp.1	1	0	0	0	0	0	0	0	1	0	1	1	4
Arhysoceble xanthopoda Moure, 1948	0	0	1	1	0	0	0	0	0	1	1	1	5
Chalepogenus unicolor Roig-Alsina, 1999	0	0	0	0	0	0	0	0	0	0	0	1	1
Lanthanomelissa aff. *clementis*	0	0	0	0	0	0	0	0	1	0	0	0	1
Lanthanomelissa betinae Urban, 1995	0	0	0	0	0	0	0	0	0	1	1	0	2
Lophopedia nigrispinis (Vachal, 1909)	1	0	1	0	0	0	0	0	0	0	1	0	3
Monoeca campestris Aguiar, 2012	1	0	0	0	0	0	0	0	0	0	0	1	2
Paratetrapedia punctata Aguiar & Melo, 2011	1	0	1	1	1	0	0	0	0	0	1	1	6
Xanthopedia iheringii (Friese,1899)	0	0	0	0	0	0	0	0	0	0	1	0	1
Xylocopini													

Ceratina (Ceratinula) sp.2	1	0	0	0	0	0	0	1	0	1	0	0	3
Ceratina (Crewella) rupestris Holmberg, 1884	0	0	0	0	0	0	0	1	1	1	1	0	4
Ceratina (Crewella) sp.2	1	0	1	1	1	1	1	1	1	1	1	1	11
Ceratina (Crewella) sp.7	0	0	0	0	0	0	0	0	1	0	1	0	2
Ceratina (Crewella) sp.8	0	0	0	0	0	0	0	0	0	0	1	1	2
Ceratina (Rhysoceratina) sp.1	1	0	1	1	1	0	0	1	1	1	1	1	9
Ceratina (Rhysoceratina) sp.3	1	0	0	1	0	0	0	1	1	1	1	0	6
Ceratina (Rhysoceratina) sp.4	1	0	0	0	0	0	0	1	1	0	1	1	5
Ceratina (Rhysoceratina) sp.5	0	0	0	0	0	0	0	0	1	0	0	1	2
Xylocopa (Nanoxylocopa) ciliata Burmeister, 1876	1	1	0	0	0	0	0	1	1	1	1	1	7
Xylocopa (Neoxylocopa) augusti Lepeletier, 1841	1	0	0	0	0	0	0	0	1	0	1	0	3
Xylocopa (Neoxylocopa) frontalis (Olivier, 1789)	0	0	0	0	0	0	0	0	0	1	1	1	3
Xylocopa (Schonnherria) macrops Lepeletier, 1841	0	0	0	0	0	0	0	0	0	0	1	0	1
COLLETINAE													
Colletini													
Colletes aff. *petropolitanus*	0	0	0	0	0	0	0	0	0	0	1	0	1
Colletes rugicollis Friese, 1900	0	0	1	0	0	0	0	0	0	0	0	0	1
Colletes sp.1	0	0	0	0	0	0	0	0	0	1	0	0	1
Colletes sp.3	0	0	0	0	0	0	0	0	1	0	0	0	1
Paracolletini													
Hexantheda missionica Ogloblin, 1948	0	1	1	0	0	0	0	0	1	1	1	1	6
Nomiocolletes sp.1	1	0	0	0	0	0	0	0	1	1	0	0	3
Xeromelissini													
Chilicola (Oediscelis) sp.1	0	0	0	0	0	0	0	1	0	0	0	0	1
HALICTINAE													
Augochlorini													
Augochlora sp.1	0	1	1	0	0	0	0	0	0	0	0	0	2

Augochlora sp.2	0	0	0	1	0	0	0	0	0	1	0	0	2
Augochlora sp.4	1	0	1	0	1	0	0	0	0	0	1	1	5
Augochlora sp.5	1	1	1	1	0	1	0	1	0	0	0	0	6
Augochlora sp.6	0	0	1	1	1	0	0	0	0	0	0	0	3
Augochlora sp.8	0	0	1	0	0	0	0	0	0	0	0	1	2
Augochlora sp.9	0	0	0	1	0	0	0	0	0	0	0	0	1
Augochlora sp.10	0	0	0	0	0	1	0	0	0	0	0	1	2
Augochlora sp.11	0	0	0	1	0	1	0	0	0	0	0	0	2
Augochlora sp.13	0	0	0	0	0	0	0	0	0	0	1	0	1
Augochlora sp.14	0	0	0	0	1	0	0	0	0	0	0	0	1
Augochlora sp.15	1	0	1	1	1	1	1	0	0	0	1	1	8
Augochloropsis aff. *cognata*	0	1	0	0	0	1	0	0	1	1	1	1	6
Augochloropsis aff. *cyanea*	0	0	0	0	0	0	0	0	0	0	1	1	2
Augochloropsis anisitsi (Schrottky, 1908)	1	1	1	1	1	1	1	1	1	1	1	1	12
Augochloropsis iris (Schrottky, 1902)	1	0	0	0	0	0	0	1	0	1	1	0	4
Augochloropsis multiplex (Valchal,1903)	1	0	1	0	0	0	0	0	0	1	1	0	4
Augochloropsis semiramis (Jörgensen, 1912)	1	0	0	1	0	1	0	1	1	1	1	1	8
Augochloropsis sp.8	1	0	1	1	1	0	0	0	0	1	1	1	7
Augochloropsis sp.10	0	0	1	0	0	0	0	0	0	1	1	1	4
Augochloropsis sp.11	1	0	0	1	0	0	1	0	0	0	1	1	5
Augochloropsis sp.12	0	0	0	1	0	0	0	0	0	0	1	1	3
Augochloropsis sp.13	0	0	0	0	0	0	0	0	0	1	0	0	1
Augochloropsis sp.14	0	0	0	0	0	0	0	1	0	0	1	0	2
Augochloropsis sp.15	0	0	0	0	0	0	0	0	1	0	0	0	1
Augochloropsis sp.16	0	0	0	0	0	0	0	0	1	0	1	0	2
Augochloropsis sp.17	0	0	1	0	0	0	0	0	0	1	1	0	3
Augochloropsis sp.18	0	0	0	0	0	0	0	0	0	0	1	0	1
Augochloropsis sp.19	0	0	0	0	0	0	0	0	0	0	1	0	1

Augochloropsis sp.20	1	0	1	1	0	0	0	0	0	0	0	0	3
Augochloropsis sp.21	1	0	1	1	1	0	0	0	0	0	0	0	4
Augochloropsis sp.22	1	0	0	0	0	0	0	0	0	0	0	0	1
Augochloropsis sp.23	1	0	1	1	0	0	0	0	0	0	0	0	3
Augochloropsis sparsilis (Vachal, 1903)	1	0	1	0	0	0	0	0	0	1	1	0	4
Augochloropsis sympleres (Vachal, 1903)	1	0	1	1	0	0	0	0	1	1	1	1	7
Ceratalictus clonius (Brèthes, 1909)	1	0	1	1	0	0	0	0	1	1	1	1	7
Ceratalictus psoraspis (Vachal, 1911)	1	0	1	0	0	0	0	0	0	1	0	1	4
Neocorynura sp.	0	0	0	0	0	0	0	0	0	0	1	0	1
Paroxystoglossa brachycera Moure, 1960	0	0	0	0	0	0	0	0	1	0	0	0	1
Paroxystoglossa jocasta (Schrottky, 1910)	0	0	0	0	0	0	3	1	0	1	1	0	6
Paroxystoglossa sp.4	0	1	0	0	0	0	0	0	0	0	0	0	1
Pseudaugochlora aff. *graminea*	1	0	1	1	1	1	0	1	1	1	1	1	10
Pseudaugochlora graminea (Fabricius, 1804)	1	0	0	0	0	0	0	1	0	0	0	0	2
Pseudaugochlora sp.1	0	0	0	0	0	1	0	0	0	1	0	0	2
Rhinocorynura inflaticeps (Ducke,1906)	1	0	0	0	1	0	0	0	1	1	1	0	5
Temnosoma sp.	0	0	0	0	0	0	0	0	0	0	1	0	1
Thectochlora basiatra (Strand, 1910)	1	0	1	1	1	0	0	0	1	1	1	1	8
Halictini													
Agapostemon (Notagapostemon) chapadensis Cockerell, 1900	1	1	1	1	1	1	1	0	1	0	0	1	9
Caenohalictus tesselatus (Moure, 1940)	0	0	0	0	0	0	0	1	0	1	0	0	2
Dialictus micheneri	1	1	1	0	0	0	0	1	1	1	1	1	8
Dialictus rostratus (Moure, 1947)	1	1	1	1	1	1	1	1	1	1	1	1	12
Dialictus sp.9	0	0	0	0	0	0	0	0	0	0	1	0	1
Dialictus sp.16	1	0	1	0	0	0	0	1	1	1	1	1	7
Dialictus sp.19	1	0	0	0	0	0	0	0	1	0	0	0	2
Dialictus sp.20	1	0	1	0	0	0	0	0	0	0	1	1	4
Dialictus sp.30	0	0	0	0	0	0	0	0	0	1	0	0	1

Dialictus sp.31	1	0	0	0	0	0	0	0	0	0	0	0	1
Dialictus sp.32	0	0	1	0	0	0	0	1	0	0	1	0	3
Dialictus sp.33	0	0	0	0	0	0	0	0	0	0	1	0	1
Dialictus sp.34	0	0	0	0	0	0	0	0	0	0	1	0	1
Dialictus sp.35	1	0	0	0	0	0	0	0	0	0	1	0	2
Dialictus sp.36	0	0	0	0	0	0	0	0	1	0	1	0	2
Dialictus sp.37	0	0	0	0	0	0	0	1	0	0	1	1	3
Dialictus sp.38	0	0	0	1	0	0	0	0	0	1	0	0	2
Dialictus sp.39	1	0	0	0	0	0	0	1	0	0	0	0	2
Dialictus sp.40	0	0	0	0	0	0	0	1	0	0	0	1	2
Dialictus sp.41	1	0	0	0	0	0	0	0	0	0	1	0	2
Dialictus sp.42	1	0	1	0	0	0	0	1	0	1	1	0	5
Dialictus sp.43	0	0	0	0	0	0	0	0	1	0	1	0	2
Pseudagapostemon (Brasilagapostemon) tesselatus Cure, 1989	1	0	0	0	1	1	1	0	1	1	1	0	7
Pseudagapostemon (Pseudagapostemon) cyaneus Moure & Sakagami, 1984	1	0	0	0	0	1	1	1	1	0	1	0	6
Pseudagapostemon (Pseudagapostemon) ochromerus (Vachal, 1904)	1	1	1	1	0	1	1	1	1	1	1	1	11
Pseudagapostemon sp.1	0	0	0	0	0	0	0	1	0	0	0	0	1
Sphecodes sp.1	0	0	0	0	0	0	0	1	0	0	0	0	1
MEGACHILINAE													
Anthidiini													
Ananthidium dilmae Urban, 1992	1	1	0	0	0	0	0	0	0	1	1	0	4
Anthidium sertanicola Moure & Urban, 1964	0	0	0	1	0	0	0	0	0	1	0	0	2
Epanthidium nectarinioides (Schrottky, 1902)	0	0	0	0	0	0	0	0	0	1	0	0	1
Megachilini													
Coelioxys (Glyptocoelioxys) aff. *cerasiopleura*	0	0	0	1	0	0	0	0	0	0	0	0	1
Coelioxys (Glyptocoelioxys) aff. *chacoensis*	1	0	0	1	0	0	0	0	1	1	1	1	6
Coelioxys (Glyptocoelioxys) cerasiopleura Holmberg, 1903	1	1	1	1	0	0	0	0	0	0	1	1	6

Coelioxys (Glyptocoelioxys) chacoensis Holmberg, 1903	1	1	1	1	0	0	0	0	0	0	0	0	4
Coelioxys (Neocoelioxys) praetextata Haliday, 1836	0	0	1	0	0	0	0	0	0	0	1	0	2
Coelioxys (Neocoelioxys) simillima Smith, 1854	0	0	0	0	0	0	0	0	0	0	0	1	1
Coelioxys (Glyptocoelioxys) sp.1	0	0	1	1	0	0	0	0	0	0	0	0	2
Coelioxys sp.1	0	0	0	0	0	0	0	0	0	0	1	0	1
Coelioxys sp.2	0	0	1	0	0	0	0	0	0	0	1	0	2
Megachile (Acentron) lentifera Vachal, 1909	1	1	1	0	0	0	0	0	0	0	1	1	5
Megachile (Austromegachile) fiebrigi Shrottky, 1908	0	1	0	0	0	0	0	0	0	0	0	0	1
Megachile (Chrysosarus) affabilis Mitchel, 1931	0	0	0	0	0	0	0	0	0	0	1	0	1
Megachile (Chrysosarus) diasi Raw, 2006	1	0	1	1	0	1	0	1	1	1	1	1	9
Megachile (Chrysosarus) inquirenda Schrottky, 1913	0	0	0	0	0	0	0	0	0	1	1	0	2
Megachile (Chrysosarus) sp.2	0	0	0	0	0	0	0	0	1	1	0	0	2
Megachile (Leptorachis) aetheria Mitchel, 1930	1	0	0	0	0	0	0	0	1	0	1	1	4
Megachile (Leptorachis) aureiventris Schrottky, 1903	1	0	1	1	0	0	0	0	1	1	1	1	7
Megachile (Leptorachis) friesei Shrottky, 1902	1	0	0	0	0	0	0	0	0	0	0	1	2
Megachile (Moureapis) apicipennis Schrottky, 1902	1	0	1	0	0	0	0	0	0	0	0	0	2
Megachile (Moureapis) maculata Smith, 1853	1	0	0	0	0	0	0	0	0	0	1	0	2
Megachile (Moureapis) nigropilosa Schrottky, 1902	1	0	1	0	0	0	0	0	0	1	1	0	4
Megachile (Pseudocentron) curvipes Smith, 1853	1	0	0	0	0	0	0	0	0	0	0	0	1
Megachile (Pseudocentron) leucopogonites Moure, 1944	1	1	0	0	0	0	0	0	0	0	0	0	2
Megachile (Pseudocentron) terrestris Shrottky, 1902	1	1	1	0	0	0	0	0	1	1	1	1	7
Megachile (Tylomegachile) orba Schrottky, 1913	0	0	0	1	0	1	0	0	1	0	0	0	3
Megachile (Acentron) sp.1	1	1	1	0	0	0	0	0	0	0	0	1	4
Megachile (Pseudocentron) sp.1	0	0	0	0	0	0	0	0	1	0	0	0	1
Megachile iheringi Schrottky, 1913	0	0	0	1	0	1	0	0	1	0	0	0	3

Appendix 3. Forbidden link trait for plants. Nr = non-restrictive; Sh = Short; M = medium; Lo = Long; S = small; La = Large.

Plant species	Main resource depht				Width of flower opening				Height of pollination chamber				Behaviour			
	Nr	Sh	M	Lo	Nr	S	M	La	Nr	S	M	La	Buzz	Oil	Strenght	none
Acisanthera alsinaefolia	1	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0
Allagoptera campestris	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1
Angelonia integerrima	0	0	1	0	0	0	0	1	0	0	0	1	0	1	0	0
Aspicarpa pulchella	1	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0
Aspilia foliacea	0	1	0	0	1	0	0	0	1	0	0	0	0	0	0	1
Aspilia montevidensis	0	1	0	0	1	0	0	0	1	0	0	0	0	0	0	1
Asteraceae sp4	0	1	1	0	1	0	0	0	1	0	0	0	0	0	0	1
Baccharis articulata	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1
Baccharis crispa	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1
Baccharis dracucunlifolia	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1
Baccharis linearifolia	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1
Baccharis myricaefolia	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1
Baccharis trilobata	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1
Baccharis uncinella	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1
Baccharis verticilata	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1
Borreria paranaensis	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1
Borreria poaya	0	1	1	0	1	0	0	0	1	0	0	0	0	0	0	1
Borreria verticilata	0	1	0	0	1	0	0	0	1	0	0	0	0	0	0	1
Buddleja elegans	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	1
Butia microspadix	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1
Byrsonima intermedia	1	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0

Byrsonima psilandra	1	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0
Calea cuneifolia	0	1	0	0	1	0	0	0	1	0	0	0	0	0	0	1
Calea hispida	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	1
Calea longifolia	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	1
Calea monocephala	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	1
Calea platylepis	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	1
Calibrachoa linoides	0	1	0	0	0	1	1	0	0	1	1	0	0	0	0	1
Chamaecrista desvauxii	1	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0
Chamaecrista punctata	1	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0
Chromolaena congesta	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	1
Chromolaena laevigata	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	1
Chrysolaena lithospermifolia	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	1
Clethra scabra	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1
Collaea speciosa	0	0	1	1	1	0	0	0	0	0	1	1	0	0	1	1
Crotalaria micans	0	0	1	1	1	0	0	0	0	0	1	1	0	0	1	1
Croton antisyphiliticus	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1
Croton heterodoxus	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1
Cuphea glutinosa	0	0	1	1	0	0	1	1	1	0	0	0	0	0	0	1
Cuphea linarioides	0	0	1	1	0	0	1	1	1	0	0	0	0	0	0	1
Disynaphia caliculata	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	1
Elephantopus mollis	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	1
Eriosema glabrum	0	1	0	0	0	0	1	1	0	0	1	1	0	0	1	1
Eriosema heterophylum	0	1	0	0	0	0	1	1	0	0	1	1	0	0	1	1
Eryngium elegans	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1
Eryngium junceum	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1
Eupatorium aff.laevigatum	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	1
Eupatorium multifidum	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	1
Galactia neesii	0	0	1	0	0	0	1	1	0	0	1	1	0	0	1	1

Galianthe elegans	0	1	1	0	1	0	0	0	1	0	0	0	0	0	0	1
Gelasine coerulea	0	0	0	1	0	0	0	1	0	0	1	0	0	1	0	1
Gochnatia polymorpha	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1
Grazielia intermedia	0	1	1	0	1	0	0	0	1	0	0	0	0	0	0	1
Heterocondylus reitzii	0	1	1	0	1	0	0	0	1	0	0	0	0	0	0	1
Hypochaeris radicata	0	1	1	0	1	0	0	0	1	0	0	0	0	0	0	1
Hyptis apertiflora	0	1	0	0	1	0	0	0	1	0	0	0	0	0	0	1
Ipomoea maurandioides	0	1	0	0	0	1	1	0	0	1	1	0	0	0	0	1
Isostigma speciosum	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	1
Jacaranda oxyphylla	0	0	0	1	0	0	1	1	0	0	1	1	0	0	0	1
Leandra simplicicaulis	1	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0
Lessingianthus argenteus	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	1
Lessingianthus grandiflorus	0	1	0	0	1	0	0	0	1	0	0	0	0	0	0	1
Lessingianthus polyphyllus	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	1
Lessingianthus simplex	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	1
Lippia hirta	0	1	1	1	1	0	0	0	1	0	0	0	0	0	0	1
Lippia lupulina	0	1	1	1	1	0	0	0	1	0	0	0	0	0	0	1
Lobelia camporum	0	0	0	1	0	0	1	1	1	0	0	0	0	0	0	1
Macroptilium prostratum	0	1	0	0	1	0	0	0	1	0	0	0	0	0	1	1
Miconia theizans	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	1
Mikania hirsutissima	0	0	1	0	1	0	0	0	0	1	1	0	0	0	0	1
Mimosa dolens var.acerba	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1
Mimosa dolens var.rudis	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1
Moritzia dusenii	0	1	1	0	0	0	1	1	1	0	0	0	0	0	0	1
Myrtaceae sp2	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1
Peltaea edouardii	0	1	0	0	0	1	1	0	0	1	1	0	0	0	0	1
Peltodon rugosus	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	1
Pfaffia tuberosa	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1

Piptocarpha axillaris	0	1	0	0	1	0	0	0	0	1	1	0	0	0	0	1
Piriqueta taubatensis	0	1	0	0	0	1	1	0	0	1	0	0	0	0	0	1
Pomaria stipularis	1	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0
Pterocaulon angustifolium	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1
Rhabdocaulon gracile	0	0	1	1	0	0	1	1	1	0	0	0	0	0	0	1
Rhabdocaulon lavanduloides	0	0	0	1	0	0	1	1	1	0	0	0	0	0	0	1
Rhamnus sphaerosperma	0	1	0	0	1	0	0	0	1	0	0	0	0	0	0	1
Salvia aliciae	0	0	1	1	0	0	1	1	0	0	1	1	0	0	0	1
Salvia lachnostachys	0	0	1	1	0	0	1	1	0	0	1	1	0	0	0	1
Senecio brasiliensis	0	0	1	1	1	0	0	0	1	0	0	0	0	0	0	1
Senecio oleosus	0	1	0	0	1	0	0	0	1	0	0	0	0	0	0	1
Sida macrodon	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1
Sida punctata	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1
Sinningia allagophylla	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	1
Sisyrhinchium micranthum	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1
Sisyrinchium brasiliense	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1
Sisyrinchium restioides	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1
Sisyrinchium vaginatum	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1
Solanum aculeatissimum	1	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0
Solanum pseudocapsicum	1	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0
Solanum reitzii	1	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0
Solidago chilensis	0	1	0	0	1	0	0	0	1	0	0	0	0	0	0	1
Stenocephalum megapotamicum	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	1
Tibouchina gracilis	1	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0
Tibouchina martialis	1	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0
Trichocline speciosa	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	1
Verbena hirta	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	1
Verbesina sordences	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	1

Vernonanthura nudiflora	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	1
Vernonanthura oligolepis	0	1	0	0	1	0	0	0	1	0	0	0	0	0	0	1
Vittetia orbiculata	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	1

Appendix 4. Forbidden link trait for bees. Nr = non-restrictive; Sh = Short; M = medium; Lo = Long; S = small; La = Large.

Bee species	Mouthpart lenght category				Intertegular distance category				Height category				Behaviour			
	Nr	Sh	M	Lo	Nr	S	M	La	Nr	S	M	La	Buzz	Oil	Strenght	None
Agapostemon chapadensis	1	1	1	0	1	1	0	0	1	0	1	0	1	0	0	1
Ananthidium dilmae	1	1	1	0	1	0	1	0	1	0	1	0	0	0	1	1
Ancyloscelis romeroi	1	1	1	0	1	0	1	0	1	1	0	0	0	0	0	1
Anthidium sertanicola	1	1	1	0	1	0	1	0	1	0	1	0	0	0	1	1
Anthophora paranensis	1	1	1	1	1	0	1	0	1	0	1	0	1	0	1	1
Anthrenoides sp.	1	1	1	0	1	1	1	0	1	0	1	0	1	0	0	1
Apis mellifera	1	1	1	0	1	0	1	0	1	0	1	0	0	0	0	1
Arhysoceble dichroopoda	1	1	1	0	1	1	1	0	1	1	0	0	0	1	0	1
Arhysoceble picta	1	1	1	0	1	1	0	0	1	1	0	0	0	1	0	1
Arhysoceble sp. 1	1	1	1	0	1	1	1	0	1	1	0	0	0	1	0	1
Arhysoceble xanthopoda	1	1	1	0	1	1	1	0	1	1	0	0	0	1	0	1
Augochlora sp. 1	1	1	1	0	1	1	0	0	1	1	0	0	1	0	0	1
Augochlora sp. 10	1	1	1	0	1	1	0	0	1	1	0	0	1	0	0	1
Augochlora sp. 11	1	1	1	0	1	1	0	0	1	1	0	0	1	0	0	1
Augochlora sp. 13	1	1	1	0	1	1	0	0	1	1	0	0	1	0	0	1
Augochlora sp. 14	1	1	1	0	1	1	0	0	1	1	0	0	1	0	0	1
Augochlora sp. 15	1	1	1	0	1	1	0	0	1	1	0	0	1	0	0	1
Augochlora sp. 2	1	1	1	0	1	1	0	0	1	1	0	0	1	0	0	1

Augochlora sp. 4	1	1	1	0	1	1	0	0	1	1	0	0	1	0	0	1
Augochlora sp. 5	1	1	1	0	1	1	0	0	1	1	0	0	1	0	0	1
Augochlora sp. 6	1	1	1	0	1	1	0	0	1	1	0	0	1	0	0	1
Augochlora sp. 8	1	1	1	0	1	1	0	0	1	1	0	0	1	0	0	1
Augochlora sp. 9	1	1	1	0	1	0	1	0	1	1	0	0	1	0	0	1
Augochloropsis aff. *cognata*	1	1	1	0	1	1	0	0	1	1	0	0	1	0	0	1
Augochloropsis aff. *cyanea*	1	1	1	0	1	0	1	0	1	1	0	0	1	0	0	1
Augochloropsis anisitsi	1	1	1	0	1	0	1	0	1	0	1	0	1	0	0	1
Augochloropsis iris	1	1	1	0	1	0	1	0	1	1	0	0	1	0	0	1
Augochloropsis multiplex	1	1	1	0	1	1	0	0	1	1	0	0	1	0	0	1
Augochloropsis semiramis	1	1	1	0	1	1	0	0	1	1	0	0	1	0	0	1
Augochloropsis sp. 10	1	1	1	0	1	1	0	0	1	1	0	0	1	0	0	1
Augochloropsis sp. 11	1	1	1	0	1	1	0	0	1	1	0	0	1	0	0	1
Augochloropsis sp. 12	1	1	1	0	1	1	0	0	1	1	0	0	1	0	0	1
Augochloropsis sp. 13	1	1	1	0	1	1	0	0	1	1	0	0	1	0	0	1
Augochloropsis sp. 14	1	1	1	0	1	1	0	0	1	1	0	0	1	0	0	1
Augochloropsis sp. 15	1	1	1	0	1	1	0	0	1	1	0	0	1	0	0	1
Augochloropsis sp. 16	1	1	1	0	1	0	1	0	1	0	1	0	1	0	0	1
Augochloropsis sp. 17	1	1	1	0	1	0	1	0	1	0	1	0	1	0	0	1
Augochloropsis sp. 18	1	1	1	0	1	0	1	0	1	1	0	0	1	0	0	1
Augochloropsis sp. 19	1	1	1	0	1	1	0	0	1	1	0	0	1	0	0	1
Augochloropsis sp. 20	1	1	1	0	1	0	1	0	1	0	1	0	1	0	0	1
Augochloropsis sp. 21	1	1	1	0	1	1	0	0	1	1	0	0	1	0	0	1
Augochloropsis sp. 22	1	1	1	0	1	1	0	0	1	1	0	0	1	0	0	1
Augochloropsis sp. 23	1	1	1	0	1	1	0	0	1	1	0	0	1	0	0	1
Augochloropsis sp. 8	1	1	1	0	1	1	0	0	1	1	0	0	1	0	0	1
Augochloropsis sparsilis	1	1	1	0	1	0	1	0	1	1	0	0	1	0	0	1
Augochloropsis sympleres	1	1	1	0	1	1	0	0	1	1	0	0	1	0	0	1

Bombus brasiliensis	1	1	1	1	1	0	1	0	1	0	1	0	1	0	1	1
Bombus morio	1	1	1	1	1	0	0	1	1	0	1	0	1	0	1	1
Bombus pauloensis	1	1	1	1	1	0	0	1	1	0	1	0	1	0	1	1
Caenohalictus tesselatus	1	1	0	0	1	1	0	0	1	1	0	0	0	0	0	1
Caenonomada labrata	1	1	1	0	1	0	1	0	1	0	1	0	0	0	0	1
Callonychium petuniae	1	1	0	0	1	1	0	0	1	1	0	0	1	0	0	1
Centris bicolor	1	1	1	1	1	0	1	0	1	0	1	0	1	0	1	1
Centris burgdorfi	1	1	1	1	1	0	0	1	1	0	0	1	1	1	1	1
Centris nitens	1	1	1	0	1	0	1	0	1	0	0	1	1	1	1	1
Centris próxima	1	0	1	1	1	0	0	1	1	0	1	0	1	1	1	1
Centris sp. 2 (aff. *C.discolor*)	1	1	1	1	1	0	0	1	1	0	0	1	1	1	1	1
Centris tarsata	1	1	1	1	1	0	1	0	1	0	1	0	1	1	1	1
Centris varia	1	1	1	1	1	0	1	0	1	0	1	0	1	1	1	1
Ceratalictus clonius	1	1	0	0	1	1	0	0	1	1	0	0	0	0	0	1
Ceratalictus psorapis	1	1	0	0	1	1	0	0	1	1	0	0	0	0	0	1
Ceratina (Ceratinula) sp. 2	1	1	0	0	1	1	1	0	1	1	0	0	0	0	0	1
Ceratina (Crewella) sp. 2	1	1	1	0	1	1	1	0	1	1	0	0	0	0	0	1
Ceratina rupestris	1	1	1	0	1	0	1	0	1	1	0	0	0	0	0	1
Ceratina sp. 1	1	1	1	0	1	1	1	0	1	1	0	0	0	0	0	1
Ceratina sp. 3	1	1	1	0	1	1	1	0	1	1	0	0	0	0	0	1
Ceratina sp. 4	1	1	1	0	1	1	1	0	1	1	0	0	0	0	0	1
Ceratina sp. 5	1	1	0	0	1	1	1	0	1	1	0	0	0	0	0	1
Ceratina sp. 7	1	1	1	0	1	1	1	0	1	1	0	0	0	0	0	1
Ceratina sp. 8	1	1	1	0	1	0	1	0	1	1	0	0	0	0	0	1
Chilicola sp. 1	1	1	0	0	1	1	0	0	1	1	0	0	0	0	0	1
Coelioxys (*G.*) sp. 1	1	1	1	0	1	0	1	0	1	0	1	0	0	0	1	1
Coelioxys aff.cerasiopleura	1	1	1	0	1	0	1	0	1	0	1	0	0	0	1	1
Coelioxys aff.chacoensis	1	1	1	0	1	0	1	0	1	0	1	0	0	0	1	1

Coelioxys cerasiopleura	1	1	1	0	1	0	1	0	1	0	1	0	0	0	1	1
Coelioxys chacoensis	1	1	1	0	1	0	1	0	1	0	1	0	0	0	1	1
Coelioxys praetextata	1	1	1	0	1	0	1	0	1	0	1	0	0	0	1	1
Coelioxys simillima	1	1	1	0	1	0	1	0	1	0	1	0	0	0	1	1
Coelioxys sp. 1	1	1	1	0	1	0	1	0	1	0	1	0	0	0	1	1
Coelioxys sp. 2	1	1	1	0	1	0	1	0	1	0	1	0	1	0	1	1
Colletes aff. *petropolitanus*	1	1	0	0	1	0	1	0	1	0	1	0	1	0	0	1
Colletes rugicollis	1	1	0	0	1	0	1	0	1	0	1	0	1	0	0	1
Colletes sp. 1	1	1	0	0	1	0	1	0	1	1	0	0	1	0	0	1
Colletes sp. 3	1	1	0	0	1	0	1	0	1	0	1	0	0	0	0	1
Dasyhalonia sp.	1	1	1	0	1	0	1	0	1	0	1	0	0	0	0	1
Dialictus micheneri	1	1	0	0	1	1	1	0	1	1	0	0	0	0	0	1
Dialictus rostratus	1	1	1	0	1	1	0	0	1	1	0	0	0	0	0	1
Dialictus sp. 16	1	1	0	0	1	1	1	0	1	1	0	0	0	0	0	1
Dialictus sp. 19	1	1	0	0	1	1	0	0	1	1	0	0	0	0	0	1
Dialictus sp. 20	1	1	0	0	1	1	0	0	1	1	0	0	0	0	0	1
Dialictus sp. 30	1	1	0	0	1	1	0	0	1	1	0	0	0	0	0	1
Dialictus sp. 31	1	1	0	0	1	1	0	0	1	1	0	0	0	0	0	1
Dialictus sp. 32	1	1	0	0	1	1	0	0	1	1	0	0	0	0	0	1
Dialictus sp. 33	1	1	0	0	1	1	0	0	1	1	0	0	0	0	0	1
Dialictus sp. 34	1	1	0	0	1	1	0	0	1	1	0	0	0	0	0	1
Dialictus sp. 35	1	1	0	0	1	1	0	0	1	1	0	0	0	0	0	1
Dialictus sp. 36	1	1	0	0	1	1	1	0	1	1	0	0	0	0	0	1
Dialictus sp. 37	1	1	0	0	1	1	0	0	1	1	0	0	0	0	0	1
Dialictus sp. 38	1	1	0	0	1	1	0	0	1	1	0	0	0	0	0	1
Dialictus sp. 39	1	1	0	0	1	1	0	0	1	1	0	0	0	0	0	1
Dialictus sp. 40	1	1	0	0	1	1	0	0	1	1	0	0	0	0	0	1
Dialictus sp. 41	1	1	0	0	1	1	0	0	1	1	0	0	0	0	0	1

Dialictus sp. 42	1	1	0	0	1	1	0	0	1	1	0	0	0	0	0	1
Dialictus sp. 43	1	1	0	0	1	1	0	0	1	1	0	0	0	0	0	1
Dialictus sp. 9	1	1	0	0	1	1	0	0	1	1	0	0	0	0	0	1
Doeringiella cingillata	1	1	1	0	1	1	0	0	1	0	1	0	0	0	0	1
Epanthidium nectarinioides	1	1	1	0	1	0	1	0	1	0	1	0	1	1	1	1
Epicharis analis	1	1	1	1	1	0	0	1	1	0	0	1	1	0	1	1
Epicharis bicolor	1	1	1	1	1	0	1	0	1	0	1	0	1	1	1	1
Epicharis iheringi	1	1	1	1	1	0	1	0	1	0	1	0	1	1	1	1
Eufriesea sp. 1	1	1	1	1	1	0	0	1	1	0	1	0	1	0	1	1
Eufriesea sp. 2	1	1	1	1	1	0	0	1	1	0	1	0	1	0	1	1
Exomalopsis analis	1	1	1	0	1	1	0	0	1	1	0	0	1	0	0	1
Exomalopsis dubia	1	1	0	0	1	1	0	0	1	1	0	0	1	0	0	1
Exomalopsis sp. 1	1	1	1	0	1	1	0	0	1	1	0	0	1	0	0	1
Gaesischia aff. *fulgurans*	1	1	1	0	1	0	1	0	1	0	1	0	0	0	0	1
Gaesischia aff. *undulata*	1	1	1	0	1	0	1	0	1	0	1	0	0	0	0	1
Gaesischia áurea	1	1	1	0	1	0	1	0	1	1	0	0	0	0	0	1
Gaesischia fulgurans	1	1	1	0	1	0	1	0	1	0	1	0	0	0	0	1
Gaesischia nigra	1	1	1	0	1	0	1	0	1	0	1	0	0	0	0	1
Gaesischia undulata	1	1	1	0	1	0	1	0	1	0	1	0	0	0	0	1
Hexanteda missionica	1	1	0	0	1	0	1	0	1	1	0	0	0	0	0	1
Isepeolus viperinus	1	1	1	0	1	1	0	0	1	0	1	0	0	0	0	1
Lanthanomelissa aff. *clementis*	1	1	1	0	1	1	0	0	1	1	0	0	0	1	0	1
Lanthanomelissa betinae	1	1	1	0	1	1	1	0	1	1	0	0	0	1	0	1
Lophopedia nigrispinis	1	1	1	0	1	1	1	0	1	1	0	0	0	1	0	1
Megachile (*A*.) sp. 1	1	1	1	0	1	0	1	0	1	0	1	0	0	0	1	1
Megachile (*P*.) sp. 1	1	1	1	0	1	0	1	0	1	0	1	0	0	0	1	1
Megachile aetheria	1	1	1	0	1	0	1	0	1	0	1	0	1	0	1	1
Megachile affabilis	1	1	1	0	1	0	1	0	1	0	1	0	0	0	1	1

Megachile apicipennis	1	1	1	0	1	0	1	0	1	0	1	0	0	0	1	1
Megachile aureiventris	1	1	1	0	1	0	1	0	1	0	1	0	1	0	1	1
Megachile curvipes	1	1	1	0	1	0	1	0	1	0	1	0	0	0	1	1
Megachile diasi	1	1	1	0	1	0	1	0	1	0	1	0	0	0	1	1
Megachile fiebrigi	1	1	1	0	1	0	1	0	1	0	1	0	0	0	1	1
Megachile friesei	1	1	1	0	1	0	1	0	1	0	1	0	0	0	1	1
Megachile iheringi	1	1	1	0	1	0	1	0	1	0	1	0	0	0	1	1
Megachile inquirenda	1	1	1	0	1	0	1	0	1	0	1	0	0	0	1	1
Megachile lentifera	1	1	1	0	1	0	1	0	1	0	1	0	0	0	1	1
Megachile leucopogonites	1	1	1	0	1	0	1	0	1	0	1	0	0	0	1	1
Megachile maculata	1	1	1	0	1	0	1	0	1	0	1	0	0	0	1	1
Megachile nigropilosa	1	1	1	0	1	0	1	0	1	0	1	0	0	0	1	1
Megachile orba	1	1	1	0	1	0	1	0	1	0	1	0	0	0	1	1
Megachile sp. 2	1	1	1	0	1	0	1	0	1	0	1	0	0	0	1	1
Megachile terrestris	1	1	1	0	1	0	1	0	1	0	1	0	0	0	1	1
Melissodes sexcincta	1	1	1	0	1	0	1	0	1	0	1	0	0	0	0	1
Melissoptila aureocinta	1	1	1	0	1	1	0	0	1	1	0	0	0	0	0	1
Melissoptila larocai	1	1	1	0	1	0	1	0	1	1	0	0	0	0	0	1
Melissoptila minimarum	1	1	1	0	1	0	1	0	1	1	0	0	0	0	0	1
Melissoptila paranaensis	1	1	1	0	1	0	1	0	1	1	0	0	0	0	0	1
Melissoptila richardiae	1	1	1	0	1	0	1	0	1	0	1	0	0	0	0	1
Melissoptila similis	1	1	1	0	1	0	1	0	1	1	0	0	0	0	0	1
Melitoma segmentaria	1	1	1	1	1	0	1	0	1	0	1	0	0	0	0	1
Mesonychium coerulescens	1	1	1	1	1	0	1	0	1	0	1	0	0	0	0	1
Mesoplia rufipes	1	1	1	0	1	0	1	0	1	0	1	0	0	1	0	1
Monoeca campestris	1	1	1	0	1	0	1	0	1	0	1	0	0	1	0	1
Neocorynura sp.	1	1	1	0	1	1	0	0	1	1	0	0	0	0	0	1
Nomiocolletes sp. 1	1	1	1	0	1	0	1	0	1	1	0	0	0	0	0	1

Osiris sp. 1	1	1	1	0	1	1	1	0	1	1	0	0	1	0	0	1
Oxaea flavescens	1	1	1	0	1	0	1	0	1	0	1	0	1	0	0	1
Paratetrapedia punctata	1	1	1	0	1	0	1	0	1	1	0	0	1	1	0	1
Parepeolus Níger	1	1	1	0	1	1	1	0	1	1	0	0	0	0	0	1
Paroxystoglossa jocasta	1	1	1	0	1	1	0	0	1	1	0	0	0	0	0	1
Paroxystoglossa sp. 4	1	1	1	0	1	1	0	0	1	1	0	0	1	0	0	1
Psaenythia annulata	1	1	1	0	1	1	1	0	1	0	1	0	1	0	0	1
Psaenythia bergii	1	1	1	0	1	0	1	0	1	0	1	0	1	0	0	1
Psaenythia collaris	1	1	0	0	1	1	0	0	1	1	0	0	1	0	0	1
Psaenythia quadrifasciata	1	1	1	0	1	0	1	0	1	1	0	0	1	0	0	1
Psaenythia sp. 2	1	1	1	0	1	0	1	0	1	0	1	0	1	0	0	1
Psaenythia sp. 3	1	1	0	0	1	0	1	0	1	1	0	0	1	0	0	1
Pseudagapostemon cyaneus	1	1	1	0	1	1	1	0	1	1	0	0	0	0	0	1
Pseudagapostemon ochromerus	1	1	1	0	1	1	0	0	1	1	0	0	0	0	0	1
Pseudagapostemon sp. 1	1	1	1	0	1	1	0	0	1	1	0	0	1	0	0	1
Pseudagapostemon tesselatus	1	1	1	0	1	1	1	0	1	1	0	0	0	0	0	1
Pseudaugochlora aff. *graminea*	1	1	1	0	1	0	1	0	1	1	0	0	1	0	0	1
Pseudaugochlora graminea	1	1	1	0	1	0	1	0	1	1	0	0	1	0	0	1
Pseudaugochlora sp. 1	1	1	1	0	1	0	1	0	1	1	0	0	1	0	0	1
Ptilothrix cfr. *plumata*	1	1	1	0	1	0	1	0	1	0	1	0	0	0	0	1
Ptilothrix fructifera	1	1	1	0	1	0	1	0	1	0	1	0	0	0	0	1
Ptilothrix plumata	1	1	1	0	1	0	1	0	1	0	1	0	0	0	0	1
Rhinocorynura inflaticeps	1	1	1	0	1	1	0	0	1	1	0	0	0	0	0	1
Rhophitulus reticulatus	1	1	0	0	1	1	0	0	1	1	0	0	0	0	0	1
Rhophitulus sp. 1	1	1	0	0	1	1	0	0	1	1	0	0	0	0	0	1
Scaptotrigona bipunctata	1	1	0	0	1	1	0	0	1	1	0	0	0	0	0	1
Schwarziana mourei	1	1	0	0	1	1	0	0	1	1	0	0	1	0	0	1
Sphecodes sp. 1	1	1	0	0	1	1	0	0	1	1	0	0	0	0	0	1

Tapinotaspoides serraticornis	1	1	1	0	1	0	1	0	1	1	0	0	0	1	0	1
Temnosoma sp.	1	1	1	0	1	1	0	0	1	1	0	0	0	0	0	1
Thalestria spinosa	1	1	1	0	1	0	1	0	1	0	1	0	0	0	0	1
Thectochlora basiatra	1	1	1	0	1	1	0	0	1	1	0	0	1	0	0	1
Thygater analis	1	1	1	1	1	0	1	0	1	0	1	0	1	0	0	1
Thygater mourei	1	1	1	1	1	0	1	0	1	0	1	0	1	0	0	1
Trigona spinipes	1	1	1	0	1	1	1	0	1	1	0	0	0	0	0	1
Xanthopedia iheringii	1	1	1	0	1	1	0	0	1	1	0	0	1	1	0	1
Xylocopa augusti	1	1	1	1	1	0	1	0	1	0	1	0	1	0	1	1
Xylocopa ciliata	1	1	1	1	1	0	0	1	1	0	0	1	1	0	1	1
Xylocopa frontalis	1	1	1	1	1	0	0	1	1	0	0	1	1	0	1	1
Xylocopa macrops	1	1	1	1	1	0	0	1	1	0	1	0	1	0	1	1